AGRICULTURAL RESEARCH INSTITUTE
PUSA

PROCEEDINGS

OF THE

GENERAL MEETINGS FOR SCIENTIFIC BUSINESS

OF THE

ZOOLOGICAL SOCIETY

OF LONDON.

1920, pp. 195–656,

WITH 14 PLATES AND 143 TEXT-FIGURES.

PRINTED FOR THE SOCIETY,
SOLD AT ITS HOUSE IN REGENT'S PARK.
LONDON:
MESSRS. LONGMANS, GREEN, AND CO.,
PATERNOSTER ROW.

LIST
OF THE
COUNCIL AND OFFICERS
OF THE
ZOOLOGICAL SOCIETY OF LONDON.
1920.

Patron.
His Majesty The King.

COUNCIL.
His Grace The Duke of Bedford, K.G., F.R.S., *President.*

The Hon. Cecil Baring, M.A.
Alfred H. Cocks, Esq., M.A.
Lt.-Col. S. Monckton Copeman, M.D., F.R.S.
Charles Drummond, Esq., *Treasurer.*
Hugh S. Gladstone, Esq., M.A., F.R.S.E.
Sir Sidney F. Harmer, K.B.E., M.A., D.Sc., F.R.S., *Vice-President.*
Prof. James P. Hill, D.Sc., F.R.S., *Vice-President.*
William Huntsman, Esq.
Prof. Ernest W. MacBride, D.Sc., LL.D., F.R.S., *Vice-President.*
Col. Sir Henry McMahon, G.C.M.G., K.C.I.E.
E. G. B. Meade-Waldo, Esq., *Vice-President.*
P. Chalmers Mitchell, Esq., C.B.E., M.A., D.Sc., LL.D., F.R.S., *Secretary.*
The Earl of Onslow, O.B.E.
Major Albert Pam.
Adrian D. W. Pollock, Esq.
His Grace The Duke of Rutland, K.G.
The Marquis of Sligo, F.S.A., *Vice-President.*
Major Richard S. Taylor.
A. Trevor-Battye, Esq., M.A.
Anthony H. Wingfield, Esq., *Vice-President.*

PRINCIPAL OFFICERS.
P. Chalmers Mitchell, C.B.E., M.A., D.Sc., LL.D., F.R.S., *Secretary.*
R. I. Pocock, F.R.S., F.L.S., *Curator of Mammals and Resident Superintendent of the Gardens.*
D. Seth-Smith, *Curator of Birds and Inspector of Works.*
Edward G. Boulenger, *Curator of Reptiles.*
Miss L. E. Cheesman, F.E.S., *Curator of Insects.*
Prof. R. T. Leiper, D.Sc., M.D., *Director of Prosectorium.*
Dr. C. F. Sonntag, Ch.B., *Anatomist.*
Dr. N. S. Lucas, M.B., Ch.B., *Pathologist.*
Dr. G. M. Vevers, M.R.C.S., L.R.C.P., *Hon. Parasitologist.*
F. Martin Duncan, F.R.M.S., *Librarian.*
F. W. Bond, *Accountant.*
W. H. Cole, *Chief Clerk.*

LIST OF CONTENTS.

1920, pp. 195–656.

EXHIBITIONS AND NOTICES.

Page

The SECRETARY. Report on the Additions to the Society's Menagerie during the month of April, 1920 437

Mr. R. I. POCOCK, F.R.S. Exhibition of, and remarks upon, a mounted specimen of a pale variety of the White-bearded Gnu (*Connochætes albojubatus*) 437

Miss JOAN B. PROCTER, F.Z.S. Exhibition of, and remarks upon, a living specimen of the tailed Batrachian *Spelerpes fuscus* Bonaparte 437

Prof. J. E. DUERDEN, F.Z.S. Exhibition of, and remarks upon, a series of lantern-slides illustrating the sexual display and nesting habits of the Ostrich 437

Prof. R. T. LEIPER, D.Sc., M.D., F.Z.S. Exhibition of lantern-slides illustrating the experimental transmission of some Helminth infections.................... 438

Dr. P. CHALMERS MITCHELL, C.B.E., M.A., LL.D., D.Sc., F.R.S. An Account, illustrated with lantern-slides, of his recent Aeroplane Trip from Cairo to Tabora... 438

The SECRETARY. Report on the Additions to the Society's Menagerie during the month of May, 1920........... 438

Prof. J. E. DUERDEN, F.Z.S. Exhibition of, and remarks upon, a series of Ostrich eggs............................ 439

Dr. R. J. TILLYARD, M.A., F.L.S. An account of the Life-history of the Dragonfly 439

The SECRETARY. Report on the Additions to the Society's Menagerie during the months of June, July, August, and September, 1920 653

Page

Dr. P. Chalmers Mitchell, C.B.E., M.A., LL.D., D.Sc., F.R.S. Exhibition of, and remarks upon, a Double-tailed Lizard 655

Mr. R. I. Pocock, F.R.S., F.Z.S. Exhibition of, and remarks upon, the skin of the groin of an example of *Tragelaphus buxtoni* 655

Mr. E. G. Boulenger, F.Z.S. Exhibition of, and remarks upon, living specimens of *Necturus* 655

Mr. T. A. Barns, F.Z.S. An Account of his recent Expedition through the Forests of Africa in search of Gorilla and Okapi 656

The Secretary. Report on the Additions to the Society's Menagerie during the month of October, 1920 656

Mr. J. T. Cunningham, M.A., F.Z.S. Exhibition of, and remarks upon, a specimen of the Leech *Trocheta*, recently found in the Society's Gardens 656

Mr. F. Martin Duncan, F.R.M.S., F.Z.S. Exhibition of, and remarks upon, a series of Cinematograph Films of Animals in the Society's Gardens 656

PAPERS.

Page

15. The Life-History and Habits of two Parasites of Blow-flies. By A. M. ALTSON. With an Introduction by Prof. H. MAXWELL LEFROY, F.Z.S. (Text-figures 1–20.) 195

16. A Revision of the Nematode Family Gnathostomidae. By H. A. BAYLIS, M.A. Oxon., Assistant in the Department of Zoology, British Museum (Natural History), and CLAYTON LANE, M.D.Lond., Lt.-Col. I.M.S. (ret.). (Text-figures 1–40; Plates I.–VIII.).. 245

17. Contributions to a Study of the Dragon-fly Fauna of Borneo.—Part IV. A List of Species known to occur in the Island. By F. F. LAIDLAW, M.A. (Cantab.), F.Z.S. (Text-figures 1–4.) 311

18. On some new Therocephalian Reptiles from the Karroo Beds of South Africa. By R. BROOM, M.D., D.Sc., F.R.S., C.M.Z.S. (Text-figures 1–9.) 343

19. Chalicotheroidea from Baluchistan. By C. FORSTER-COOPER, M.A., F.Z.S., Superintendent of the University Museum of Zoology, Cambridge. (Plate I. and Text-figures 1–7.) 357

20. Fauna of Western Australia.—III. Further Contributions to the Study of the Onychophora. The Anatomy and Systematic Position of West Australian *Peripatoides*, with an account of certain histological details of general importance in the study of Peripatus. By WM. J. DAKIN, D.Sc., F.Z.S., F.L.S., Professor of Biology, University of Western Australia. (Plates I.–V.) 367

21. Notes on Marine Wood-boring Animals.—I. The Ship-worms (Teredinidae). By W. T. CALMAN, D.Sc. (Text-figures 1–11.) 391

22. Report on Entozoa collected from Animals which died in the Zoological Gardens of London during eight months of 1919–20. By G. M. VEVERS, M.R.C.S., L.R.C.P., F.Z.S., Beit Memorial Research Fellow, Demonstrator in Helminthology at London School of Tropical Medicine, and Hon. Parasitologist to the Zoological Society of London 405

Page

23. On a Collection of Tailless Batrachians from East Africa made by Mr. A. Loveridge in the years 1914–1919. By Miss JOAN B. PROCTER, F.Z.S. (Text-figures 1–4.) 411

24. On the Type-specimen of *Rana holsti* Boulenger. By Miss JOAN B. PROCTER, F.Z.S. (Text-figure 5.) 421

25. On the External and Cranial Characters of the European Badger (*Meles*) and of the American Badger (*Taxidea*). By R. I. POCOCK, F.R.S. (Text-figures 19–25.) 423

26. On some Results of Ligaturing the Anterior Abdominal Vein in the Indian Toad (*Bufo stomaticus* Lütken). By W. N. F. WOODLAND, D.Sc.(Lond.), F.Z.S., Indian Educational Service, Senior Professor of Zoology Muir Central College, Allahabad, U.P., India. (Text-figure 1.) 441

27. Some Observations on the Structure and Life-History of the Common Nematode of the Dogfish (*Scyllium canicula*). By J. H. LLOYD, M.Sc., F.Z.S., Assistant Lecturer and Demonstrator in Zoology at University College, Cardiff. (Text-figures 1–3.).................... 449

28. On the Sexual Phase in certain Indian Naididæ (Oligochæta). By HARU RAM MEHRA, M.Sc., Professor of Zoology, Hindu University, Benares. (Text-figures 1–3.) 457

29. Observations on the Flight of Flying-Fishes. By E. H. HANKIN, M.A., Sc.D., Agra, India. (Text-figures 1–2.) 467

30. Observations on the Life-History, Biology, and Genetics of the Lady-bird Beetle, *Adalia bipunctata* Mulsant. By ONERA A. MERRITT HAWKES, M.Sc.(Birm.), B.Sc. (Lond.) 475

31. Filariid Worms from Mammals and Birds in the Society's Gardens, 1914–1915. By C. L. BOULENGER, M.A., D.Sc., F.Z.S., Professor of Zoology, University of the Punjab, Lahore. (Text-figures 1-12.) 491

32. The Fauna of the African Lakes; a Study in Comparative Limnology with special reference to Tanganyika. By WM. A. CUNNINGTON, M.A., Ph.D., F.Z.S. (Text-figures 1–2.) 507

33. Descriptions of the Adult, Larval, and Pupal Stages of a New Mosquito from Lord Howe Island, S. Pacific. By HENRY F. CARTER, Liverpool School of Tropical Medicine. (Text-figures 1–3.) 623

Page

34. The Life-History and Habits of the Yellow Dung-Fly (*Scatophaga stercoraria*): a possible Blow-Fly Check. By G. S. Cotterell. With a Preface by Prof. Maxwell Lefroy, F.Z.S. (Text-figures 1–14.) 629

35. Remarks on the Respiratory Movements of *Necturus* and *Cryptobranchus*. By A. Willey, M.A., D.Sc., F.R.S., F.Z.S. 649

Alphabetical List of Contributors................................ viii

Index of Illustrations xiii

Index xv

ALPHABETICAL LIST

OF THE

CONTRIBUTORS,

With References to the several Articles contributed by each.

(1920, pp. 195–656.)

Page

ALTSON, A. M.

The Life-History and Habits of two Parasites of Blow-Flies. With an Introduction by Prof. H. MAXWELL LEFROY, F.Z.S. (Text-figures 1–20.) 195

BAYLIS, H. A., M.A. (Oxon.), Assistant in the Department of Zoology, British Museum (Natural History), and LANE, CLAYTON, M.D.(Lond.), Lt.-Col. I.M.S. (ret.).

A Revision of the Nematode Family Gnathostomidæ. (Plates I.–VIII.; Text-figures 1–40.) 245

BOULENGER, C. L., M.A., D.Sc., F.Z.S., Professor of Zoology, University of the Punjab, Lahore.

Filariid Worms from Mammals and Birds in the Society's Gardens, 1914–15. (Text-figures 1–12.) 491

BOULENGER, E. G., F.Z.S., Curator of Reptiles.

Exhibition of, and remarks upon, living specimens of *Necturus* 655

BROOM, R., M.D., D.Sc., F.R.S., C.M.Z.S.

On some new Therocephalian Reptiles from the Karroo Beds of South Africa. (Text-figures 1–9.) 343

Page

Calman, W. T., D.Sc.

Notes on Marine Wood-boring Animals.—I. The Ship-Worms (Teredinidæ). (Text-figures 1–11.) 391

Carter, H. F., Liverpool School of Tropical Medicine.

Descriptions of the Adult, Larval, and Pupal Stages of a New Mosquito from Lord Howe Island, South Pacific. (Text-figures 1–3.) 623

Cotterell, G. S.

The Life-History and Habits of the Yellow Dung-Fly (*Scatophaga stercoraria*); a possible Blow-Fly Check. With a Preface by Prof. H. Maxwell Lefroy, F.Z.S (Text-figures 1–14.) 629

Cunningham, J. T., M.A., F.Z.S.

Exhibition of, and remarks upon, a specimen of the Leech *Trocheta*, recently found in the Society's Gardens. 656

Cunnington, Wm. A., M.A., Ph.D., F.Z.S.

The Fauna of the African Lakes; a Study in Comparative Limnology with special reference to Tanganyika. (Text-figures 1–2.) 507

Dakin, Wm. J., D.Sc., F.Z.S., F.L.S., Professor of Biology, University of Western Australia.

Fauna of Western Australia.—III. Further Contributions to the Study of the Onychophora. The Anatomy and Systematic Position of West Australian *Peripatoides*, with an account of certain histological details of general importance in the study of Peripatus. (Plates I.–V.)... 367

Duerden, J. E., F.Z.S.

Exhibition of, and remarks upon, a series of lantern-slides illustrating the sexual display and nesting habits of the Ostrich... 437

Exhibition of, and remarks upon, a series of Ostrich eggs 439

Page

Duncan, F. Martin, F.R.M.S., F.Z.S., Librarian to the Society.

Exhibition of, and remarks upon, a series of Cinematograph Films of Animals in the Society's Gardens 656

Forster-Cooper, C., M.A., F.Z.S., Superintendent of the University Museum of Zoology, Cambridge.

Chalicotheroidea from Baluchistan. (Plate I.; Text-figures 1–7.) 357

Hankin, E. H., M.A., Sc.D., Agra, India.

Observations on the Flight of Flying-Fishes. (Text-figures 1–2.) 467

Hawkes, Onéra A. Merritt, M.Sc.(Birm.), B.Sc.(Lond.).

Observations on the Life-History, Biology, and Genetics of the Lady-bird Beetle, *Adalia bipunctata* Mulsant 475

Laidlaw, F. F., M.A.(Cantab.), F.Z.S.

Contributions to a Study of the Dragonfly Fauna of Borneo.—Part IV. A List of Species known to occur in the Island. (Text-figures 1–4.) 311

Lane, Clayton, M.D.(Lond.), Lt.-Col. I.M.S.(ret.).

See Baylis, H. A.

Lefroy, H. Maxwell, F.Z.S.

See Altson, A. M.

See Cotterell, G. S.

Leiper, R. T., D.Sc., M.D., F.Z.S.

Exhibition of lantern-slides illustrating the experimental transmission of some Helminth infections......... 438

Page

LLOYD, J. H., M.Sc., F.Z.S., Assistant Lecturer and Demonstrator in Zoology at University College, Cardiff.

Some Observations on the Structure and Life-History of the Common Nematode of the Dogfish (*Scyllium canicula*). (Text-figures 1–3.) 449

MEHRA, HARU RAM, M.Sc., Professor of Zoology, Hindu University, Benares.

On the Sexual Phase in certain Indian Naididæ (Oligochæta). (Text-figures 1–3.) 457

MITCHELL, P. CHALMERS, C.B.E., M.A., D.Sc., LL.D., F.R.S., Secretary to the Society.

Report on the Additions to the Society's Menagerie during the month of April, 1920 437

An Account, illustrated by lantern-slides, of his recent Aeroplane Trip from Cairo to Tabora 438

Report on the Additions to the Society's Menagerie during the month of May, 1920 438

Report on the Additions to the Society's Menagerie during the months of June, July, August, and September, 1920 653

Exhibition of, and remarks upon, a Double-tailed Lizard 655

Report on the Additions to the Society's Menagerie during the month of October, 1920 656

POCOCK, R. I., F.R.S., F.Z.S., Curator of Mammals and Resident Superintendent of the Gardens.

On the External and Cranial Characters of the European Badger (*Meles*) and of the American Badger (*Taxidea*). (Text-figures 19–25.) 423

Page

Pocock, R. I. (*cont.*).

Exhibition of, and remarks upon, a mounted specimen of a pale variety of the White-bearded Gnu (*Connochætes albojubatus*) 437

Exhibition of, and remarks upon, the skin of the groin of an example of *Tragelaphus buxtoni* 655

Procter, Miss Joan B., F.Z.S.

On a Collection of Tailless Batrachians from East Africa made by Mr. A. Loveridge in the years 1914–1919. (Text-figures 1–4.) 411

On the Type-specimen of *Rana holsti* Boulenger. (Text-figure 5.) 421

Exhibition of, and remarks upon, a living specimen of the tailed Batrachian *Spelerpes fuscus* Bonaparte 437

Tillyard, R. J., D.Sc., M.A., F.L.S.

An account of the Life-History of the Dragonfly 439

Vevers, G. M., M.R.C.S., L.R.C.P., F.Z.S., Hon. Parasitologist to the Society.

Report on Entozoa collected from Animals which died in the Zoological Gardens, London, during eight months of 1919–1920 405

Willey, A., M.A., D.Sc., F.R.S., F.Z.S.

Remarks on the Respiratory Movements of *Necturus* and *Cryptobranchus* 649

Woodland, W. N. F., D.Sc.(Lond.), F.Z.S., Indian Educational Service, Senior Professor of Zoology, Muir Central College, Allahabad, U.P., India.

On some Results of Ligaturing the Anterior Abdominal Vein in the Indian Toad (*Bufo stomaticus* Lütken). (Text-figure 1.) 441

PROCEEDINGS

OF THE

GENERAL MEETINGS FOR SCIENTIFIC BUSINESS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.

PAPERS.

15. The Life-History and Habits of two Parasites of Blow-flies. By A. M. ALTSON. With an Introduction by Prof. H. MAXWELL LEFROY, F.Z.S.*

[Received March 29, 1920: Read April 13, 1920.]

(Text-figures 1–20.)

INDEX.

Page

A Short Account of the Start of the Work 196

Breeding Methods 198

Life-History and Habits of *Alysia manducator* Panz. and Hosts 199

Life-History and Habits of *Nasonia brevicornis* Ashm. and Hosts ... 216

Super-parasitism, or Accidental Secondary Parasitism 230

Refrigerating Experiment 240

Conclusions upon the Economic Importance of *A. manducator* Panz. and *N. brevicornis* Ashm. 241

Summary 242

Acknowledgments 243

References 243

INTRODUCTION.

This paper deals with part of the work initiated after a visit to Australia, where the lack of any means of control of the Sheep Blow-flies is painfully evident. As some of these probably came from England, it seemed desirable to study the natural checks that keep down the pest here: and the accidental discovery at the Society's Gardens of three important checks gave the work a start. In this communication two Hymenopterous parasites are discussed: other parasites are under investigation.

---

* Communicated by Prof. LEFROY.

Acknowledgments are due to the Australian Commonwealth Government for a small grant to assist the work.

H. M. LEFROY.

A SHORT ACCOUNT OF THE START OF THE WORK.

About the last week in June Prof. Maxwell Lefroy gave the writer a tin containing approximately 1500 Dipterous puparia to breed out. These had been forwarded by Miss Cheesman, the Society's Assistant Curator of Insects.

The contents of the tin were divided into five lots, and put into an equal number of jars containing damped soil. The jars were covered with muslin. (At the outset, it should be explained that occasional damping of soil was necessitated by the fact that the soil was kept in sacks in the laboratory, and consequently any moisture originally in it soon evaporated.)

Adult flies began to emerge a week later, and continued to do so for a period of six or seven days. They were identified as *Calliphora erythrocephala* Meig.

The jars containing the empty puparia and a large number of intact puparia were then put aside. They were occasionally examined, and on 14th July the first jar inspected was found to contain an active Hymenopteron, which upon closer observation appeared to be a female Braconid; the examination of the other four jars showed that three of them also contained specimens of the Braconid. As the remaining jar did not contain any Braconid, the contents were emptied and carefully examined; all empty puparia were separated from those which were still intact, and six of the latter were opened, with the result that two were found to contain fully-formed flies which had failed to emerge, another a shapeless, smelling, moist mass—an atrophied fly-nymph—and the other three contained Braconids, one in an early pupal state, the others fully-formed adults apparently ready for emergence, free of the pupal skin, and wings fully expanded *.

With the appearance of this parasite, breeding experiments were commenced. The Braconids were released in a muslin-covered glass cylinder, which was placed in a large tray containing soil. Food was put in.

Blow-fly larvæ and eggs were obtained by exposing meat at the Zoological Gardens and on the balcony of the Imperial College of Science, South Kensington, and a test made to ascertain if the Braconids would parasitize the larvæ. The test was satisfactory, and one female began ovipositing one minute after the admission of the larvæ, and in 25 minutes five females were at work.

---

* Both insects crawled out of their opened puparium; one at once passed the meconium and discharge, the other did not: both were males. The former lived a normal period, the latter was dead on the second day.

Numbers of the parasite were emerging from the jars at this time, and a large cage was brought into use to contain them. As it was desirable to obtain as many adults as possible, a search was made at the Society's Gardens at the spot where the original material was found, and a further supply of puparia obtained. Whilst sorting out this material preparatory to putting the intact puparia into jars, a number of Chalcids were observed crawling about on the soil. Most of these were captured. A closer scrutiny of the puparia disclosed minute holes in several and Chalcids emerging from some of them; it was also noticed that a few puparia showed that Braconids had emerged from them. In view of the appearance of this Chalcid, each puparium—they were of a *Calliphora* species and presumably *erythrocephala*, the same species as the flies—was placed in a separate tube. Both parasites continued to emerge from this material daily for a period of twelve days.

As no Chalcids appeared from the original material, which had been in the jars for nearly a month, it was evident that they had carried out their attack after the original material had been removed; and as this consisted entirely of puparia, it seemed reasonable to assume that this Chalcid parasitized the pupal stage. This supposition proved correct, and will be referred to later.

A constant supply of blow-fly material for parasitization was maintained by putting small receptacles containing meat out in the open and placing it under control as soon as eggs had been deposited on it. No opportunity occurred at this time to obtain meat blown by flies of definite species under control; but with this object in view, small quantities of the larvæ from each lot of blown material were segregated and allowed to develop into adults, when their species were determined, and they were then placed under control in separate cages.

In the hope that the Braconid was still about, and in order to obtain large numbers of them, receptacles containing soil and meat were put out in the vicinity of the spot from which the original material was obtained; this, Miss Cheesman kindly undertook to do, and the receptacles were left in the open until the blow-fly larvæ had commenced pupation, when the material was removed to the laboratory to be bred out. It was at once observed that the large parasite was still about. It was seen to come to the receptacles and to attack the larvæ. Whilst this was being done, Prof. Lefroy put receptacles out at Heston to see if the parasites could be obtained in this locality. Only the Braconid parasite appeared from the latter place.

All lots of material obtained from Regent's Park and Heston were bred out to observe if any parasites other than the Braconid and Chalcid made their appearance: none did.

By the end of August large numbers of the parasites were in the cages in the laboratories and extensive breeding operations in progress, and every effort was made to maintain a constant supply of active parasites so that by the end of the year there would exist a large stock of hibernating material.

It was not until October that the writer took specimens of the parasites to Mr. J. Waterston at the Natural History Museum for identification. The Braconid was identified as *Alysia manducator* Panz. and the Chalcid as *Nasonia brevicornis* Ashm. Mr. Waterston kindly brought to the writer's notice a paper by Graham-Smith (**1**) in which these parasites were referred to. Up to this time no reference to the Braconid was known, and that the Chalcid should prove to be *Nasonia brevicornis* was not anticipated, especially as the illustrations in Australian publications in the writer's possession depicted a female of this species walking with an extruded ovipositor, a position which it only assumes in death.

BREEDING METHODS.

After the first lots of the parasites had completed their work, the several species of blowflies, which had been obtained from the meat exposed in different localities, were segregated.

The species obtained were :—

Blue Bottle....................	*Calliphora erythrocephala* Meig.
,, ...	,, *vomitoria* Linn.
British Sheep Maggot-fly ...	*Lucilia sericata* Meig.
Green Bottle	,, *cæsar* Linn.
Green Bottle	*Phormia grœnlandica* Ztt.

In addition to these, the Common House-fly, *Musca domestica* Linn., which is constantly bred at the College, was available.

Upon Prof. Lefroy's advice as to the best medium in which to breed the larvæ, ox liver was used, and found very satisfactory. A somewhat important point in this connection was that liver could be procured easily as it did not fall within the scope of the "Meat Rationing Order."

The liver was cut into small pieces, placed in glass receptacles and put into the cages containing the different species of "blowflies." As soon as it had been blown—that is, eggs deposited on it—the receptacle was withdrawn and emptied into a glass dish, in which additional pieces of liver were put when the eggs hatched. The receptacles were refilled and put back into the cages when more eggs were required; this method was continued as long as larvæ or puparia have been required. The glass dishes with the newly-hatched larvæ were placed in large trays of 18 inches diameter and 4 inches height, and which contained finely sifted sand or soil to a depth of 2 to 3 inches. It was found that the full-grown larvæ invariably crawled out of the glass dishes, and after roaming about on the sand, proceeded to disappear and pupate.

This method of breeding the blow-flies was successful with all species except *Lucilia sericata*; the original lot of these were obtained from the fleece of a "struck" sheep. A piece of sheep's skin was obtained consisting of the tail and the whole of the anal area with a quantity of fæces adhering to it, and was placed on a piece of liver on fine damped soil in a tray; artificial heating was applied, and the species was successfully reared by this means.

Several methods of presenting the larvæ for parasitization were tried, the original object being the attainment of those conditions in which they would be an easy prey for the Braconid's attack. It was found that free larvæ severely damaged the females, so that it became necessary to reproduce conditions as nearly natural as possible.

In the case of the Chalcid, host puparia—in a proportion of 20 per female—were placed in small receptacles in the cages and left there for ten days for parasitization. The puparia were obtained from the trays by sifting; this rough handling did no appreciable damage.

The breeding operations were in progress from July to the end of December; from July to the middle of September all lots of parasitized material were reared to maintain supplies of parent generations for the cages; after this period the parasitized material was exposed on the balcony of the College to hibernate and form the necessary stock for shipment.

LIFE-HISTORY AND HABITS OF *ALYSIA MANDUCATOR* PANZ., AND HOSTS.

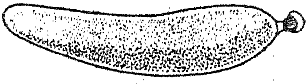
Introductory.—*Alysia manducator* Panz. was selected by Latreille as the type of his genus *Alysia*, and belongs to the group *Exodontes* of the family Braconidæ.

It should be noted that the following account is mainly based upon observations of this insect in captivity; opportunities to observe it under natural conditions were very limited.

The Length of the Life-cycle.—The length of the life-cycle from egg to adult is, under suitable conditions of temperature, from 33 days and upwards, with a mean average of 52 days, but varies considerably for some reason even amongst those of the same parent and under the same conditions. Table I. shows this extraordinary variation, and refers to nine lots of material parasitized in the laboratory. Graham-Smith (**1**) records an instance in which the life-cycle took only 25 days.

The Egg.—The egg (text-fig. 1) is very small, cylindrical, tapering, and broadly rounded at one extremity, broadest at the other with the micropyle narrowly attached and having the appearance of a large protuberance. It is just visible to the

Text-figure 1.



Egg of *A. manducator*, from ovary. Size ·675×·150 mm. ×61. Original.

Table I.—Showing variations in length of life-cycle.

Alysia manducator.

Dates of first and last emergence of adults.	Nos. of Jars containing parasitized material and dates when parasitized.									Daily Temp. to nearest degree Cent.
	No. 1. 17/7/19	No. 2. 18/7/19	No. 3. 18/7/19	No. 4. 19/7/19	No. 5. 21/7/19	No. 6. 21/7/19	No. 7. 31/7/19	No. 8. 31/7/19	No. 9. 6/8/19	
Aug. 18	↑									25
19										24
20										22
21										22
22										19
23										22
24										19
25										18
26										18·5
27										17·5
28										16
29										19
30										17·5
31										19
Sept. 1										17
2										18·5
3										19
4										21·25
5			↑							24
6		↑								22·5
7				↑		↑				21
8										22·5
9										24
10										25
11		↓			↑					27
12	↓		↓	↓			↑			27
13								↑		19
14					↓	↓				18
15									↑	17
16										17
17										20
18										21
19										18
20										18
21										18
22										18·5
23										19 *
24										20
25								↓		21
26										20
27										20
28										20
29										19·5
30										19·5
Oct. 1										20
2										20
3										20
4										19·5
5										20
6							↓			20
7										20
8										19
9										20
10										20
11										19·5
12									↓	20

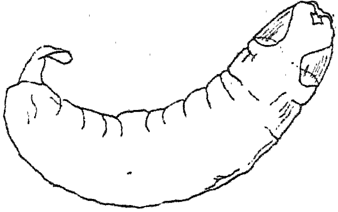
* Artificial heating from 23rd Sept.

Thus, contents of No. 1 Jar took to complete cycle 33–58 days; No. 2, 51–56 days; No. 3, 50–57 days; No. 4, 51–56 days; No. 5, 53–55 days; No. 6, 49–55 days; No. 7, 44–68 days; No. 8, 45–57 days; No. 9, 40–69 days: giving a general average of 46$\frac{2}{3}$–59 days with a mean average of 52.

naked eye. It is translucent white, with a smooth glossy surface. The time required for the egg to hatch varies, and in an investigation into this point active first instar larvæ were found in the hosts, which had pupated 66 hours after the eggs were deposited, the temperature during this time being 20° C. But, that the egg hatches in from 30 to 50 hours generally is obvious from the condition of the host pupa, which is either in a state of histolysis or an early stage of histogenesis; and also by the occasional distorted appearance of the host puparium. The egg is deposited in any part of the larval host, and this lack of discrimination accounts for the non-appearance of the parasite on occasions. If, for instance, the egg was lodged amongst muscles, it would be crushed by the movements of the host larva; this point is mentioned again under *Oviposition*.

The Larva.—The first instar larva (text-fig. 2) differs in appearance from the later instars, particularly in the shape and appearance of its head, which is a thickly chitinized brownish capsule fitted with a stout pair of mandibles, and has a pair of small protuberances on the dorsal surface, the antennæ. It consists, apparently, of 14 segments including the head; the abdomen terminates in a "tail"-like appendage, the abdominal vesicle. A similar organ in *Microgaster*, and other endo-parasitic Hymenoptera, Gatenby (5) concludes is respiratory in function. That this is the function of this organ in *A. manducator* appears very probable, and it presumably functions by means of osmosis.

Text-figure 2.



First instar larva of *A. manducator*. Camera-lucida drawing, partly reconstructed. ×41. Original.

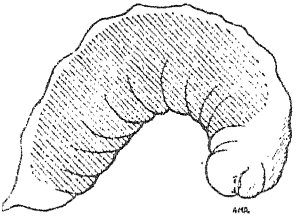
Since the larva sometimes hatches in the body of its larval host before histolysis has begun, its head seems well adapted to enable it to move in the host pupa if it hatches—as it usually does—during the process of histolysis or that of histogenesis.

What part of the host forms the food of the various instars has not been observed, but it must consist of liquid or semi-liquid, and in the first instar would probably be the body-fluid and fat-bodies; and the later instars would feed on those systems which have ceased breaking down or building up after the original attack of the first instar larva. That the larva sometimes hatches before the host pupates is evidenced by the fact that a puparium containing the parasite occasionally bears a distorted appearance—indicating the severance of a muscle—or is shrivelled and excessively wrinkled (text-fig. 8).

The first instar larva, with the exception of its brownish head, is translucent white and glabrous throughout; the integument is very soft and easily damaged.

Text-fig. 3 illustrates a larva of the second instar, in which the capsule head has disappeared and has given place to one the type of which remains constant in the later instars. The particular larva illustrated was removed from a *Calliphora* sp. puparium, and was placed in a watch-glass containing three macerated fly-nymphs with a few drops of water added to reduce the density, and with the aid of a microscope it was kept under observation for more than half-an-hour whilst feeding. The larva remained quite motionless during this time, its mouth-parts alone were constantly working; no movement of the mandibles was observed, but the extensive lip-like labium was seen to be continually moving with a "rippling" action whilst the liquid was being absorbed. The abdominal vesicle has proportionately shortened. The mid-intestine now shows up clearly, swollen with food and giving a pale yellow colour to the larva.

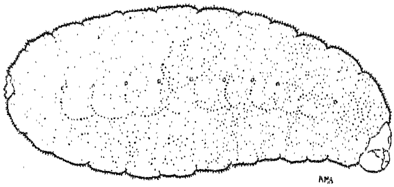
Text-figure 3.



Second instar larva of *A. manducator*. Greatly magnified. Original.

The intermediate instars show no superficial difference from the second, beyond the shortening of the "tail"-like abdominal vesicle and the increase in the size of the larva and corresponding swelling of the mid-intestine.

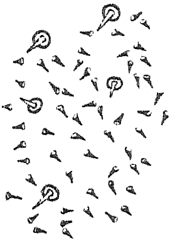
Text-figure 4.



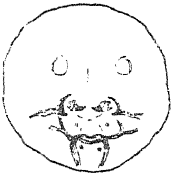
Full-grown larva of *A. manducator*. Greatly magnified. Length 4·25 mm. Original.

The last instar larva (text-fig. 4) differs from the preceding instars in that—with the exception of the cephalic and posterior segments—the integument is covered with fine setæ and scattered sensory hairs (text-fig. 5). The mouth-parts of this stage are well defined (text-fig. 6). The posterior appendage has almost disappeared; easily visible just under the integument and scattered about in the abdominal region are large white particles. The spiracles, which are of a very simple structure, number nine pairs, and appear on the second thoracic and first eight abdominal segments. There appears, on either side, a small main trachea with segmental branches.

Text-figure 5.



Text-figure 6.



Text-fig. 5.—Setæ and sensory hairs on portion of integument of full-grown larva of *A. manducator*. Greatly magnified. Original.

Text-fig. 6.—Head of full-grown larva, partly reconstructed, camera-lucida drawing. × 25. Original.

During all the larval stages the mid-intestine is closed caudally, and it is not until the emergence of the adult insect that the residuary and undigested food-matter is voided.

The last instar larva has, on several occasions, been observed feeding upon the liquid remnants of its host, having at some stage pushed the tracheæ of the host to the sides of the puparium; the latter being lined with the fly-nymph's pupal skin. It seems only reasonable to assume that chitin, represented by the integument of the fly pupa, and the main tracheal trunks of the blow-fly larva which remain constant in histolysis do not form part of the larval diet. This postulation, if correct, would exempt the Braconid larva from the necessity of eating its own cast larval skins.

Before the pro-pupal stage, the final instar larva—which by this time completely occupies the puparium of its host—spins a silken cocoon, which either adheres (*a*) to the thick chitinized walls of the puparium, or (*b*) to the stretched integument of the fly pupa, and which generally is caused to adhere to the walls of the puparium. In (*a*) the absence of the fly-pupal skin would be accounted for by the first instar larva having started its attack before the host larva had settled down to pupate or before histogenesis had started, and (*b*) after histogenesis had started. So that the texture of this cocoon or lining to the puparium is not always the same, the external portion of it—that which is in contact with the fly puparium—may be silk or pupal integument, and in those cases examined the tracheal system was visible either outside the silk or between the silk and pupal integument; no cast skins however were detected, the search was not very thorough. Sometimes the cocoon with the fly-pupal integument shows the outline of the fly-nymph's legs etc., indicating late hatching of the egg and after histogenesis had proceeded some time.

The spinning of this cocoon raises an interesting point as to the means whereby the larva, which appears to fill the puparium, is able to move about within it, to accomplish the task of covering every part of the inside, and also of absorbing the liquid remains of the fly-nymph, taking into consideration that its intestine is now filled with a semi-solid mass of undigested fly-pupa. It has been observed that the spinning of the cocoon reduces the size of the larva to some extent, but observation has not definitely established the means adopted; some larvæ have been found contracted into a small compass as though able to revolve within the puparium and thus change their direction, whilst others appear to be working in the manner common amongst silk-spinning Lepidopterous larvæ. The latter method is the most probable, and is supported by the appearance of the larva.

The lining strengthens the puparium considerably, and is a sure indication of the presence of the parasite in its last stages. It is weakest at the anterior end of the host puparium, where the chitinized mouth-parts of the blow-fly larva form an obstruction.

The length of larval life in the different instars appears to vary considerably, but no details were obtained; in one instance, however, a full-grown larva was found in a puparium 18 days after the egg was deposited. This is the shortest period recorded. On the other hand, some intact puparia, which were from a lot parasitized on 6th August, were opened on 26th November, and 13 were found to contain full-grown healthy larvæ, 112 days after the eggs were deposited. The final instar larva is the stage where the great variations in the life-cycle occurs. The time taken to pass from this stage to that of the pupa varies from a few days to many months. This point has been observed by Graham-Smith (**1**), who also observed in 1915 that from material parasitized in 1914, "the individuals emerging in the spring were much larger than those which emerged in the autumn." This and the observations made during the course of this work have caused the writer to form the opinion that among the factors responsible—beyond the question of food-supply—is that of the size of the host puparium. The integument of the puparium of an undersized blow-fly larva is much thinner than that of the full-grown larva, consequently the parasite within the former is more susceptible to the variations of the temperature, which alone would retard development.

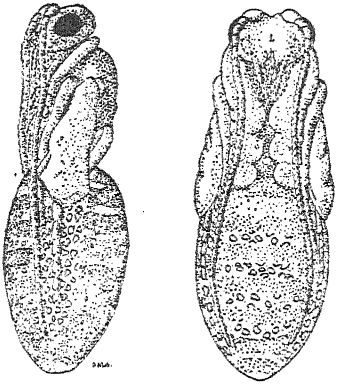
In size the full-grown larvæ vary considerably, but this is naturally dependent upon the size of the host.

The pro-pupal stage, *i. e.* after spinning the cocoon, may last a few days or several months. In two specific instances observed the pro-pupa changed to the pupa, the one 2 days after it was exposed in the puparium, the other 5 days after.

Some hibernating larvæ from the stock have been observed in puparium which they had not yet lined, although four months had elapsed since the date of oviposition.

The Pupa.—The pupa (text-fig. 7) is loose within the cocoon, and is capable of slight movement. The meconium now appears to become slightly compressed, due to the process of metamorphosis.

Text-figure 7.



Lateral and ventral aspect of pupæ of *A. manducator*. Greatly magnified. The figure on left a few days older than that on right. Original.

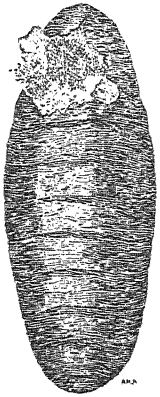
During the whole pupal stage the afore-mentioned large white particles are visible, at first scattered about in the abdomen and later can be seen between the tergites and sternites.

The pupa, which is glabrous throughout, is, at first, creamy white with reddish-brown eyes and ocelli, in a few days the head and thorax turn grey, gradually becoming black; meanwhile, the sternites and tergites—widely separated over the distended abdomen—begin to turn grey, and the eyes and ocelli darken; the legs and antennæ similarly begin to show the coloration of the adult, likewise the mouth-parts. The last larval skin splits across the head dorso-ventrally backwards, and then apparently slips back to the apex of the abdomen, from which it is disengaged by movements of the abdomen and antennæ of the male or the ovipositor of the female. In no instance has the larval exuvium been found attached to the pupa, but lying in a crumpled mass beyond the apex of its abdomen.

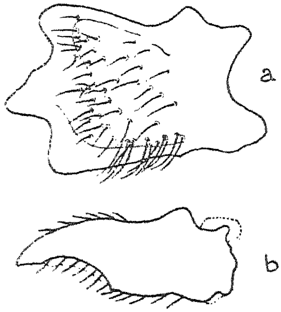
The length of the pupal stage was, in two specific instances, found to be 7 and 10 days respectively with a mean temperature of 21° C., but lengthens considerably in a low temperature; although this will not delay indefinitely the emergence of the adult, which either emerges upon the slightest increase in the temperature, or, in the event of a steady and prolonged decrease, dies within the puparium.

The Adult.—The adult emerges from the host puparium and its cocoon by breaking away that part directly in contact with the head (text-fig. 8). It is furnished with a very powerful pair of mandibles (text-fig. 9, *a*) beautifully adapted for the work in hand. It breaks away the cocoon and puparium by an outward movement, and does not bite the obstruction. Text-fig. 9, *b* illustrates the outline of a section through the centre of a mandible, and shows its scoop-like appearance ventro-dorsally. In the outward movement of the mandibles a small fracture appears on the puparium, generally between the second and fourth segment, gradually increasing in size until the perfect insect has created an aperture large enough to enable it to escape. Observation has failed to disclose any use for the mandibles other than breaking out of the host puparium, which operation, when in progress by several insects, has been distinctly audible by putting the ear over the mouth of the jar in which they were confined. It is worthy of note that the mechanism of the mandibles must be diametrically opposed to that of most insects, but upon consideration it seems obvious that by no other means could so large a parasite escape from the puparium, which presents to it a concave surface.

Text-figure 8.



Text-figure 9.



Text-fig. 8.—Shrivelled and wrinkled puparium from which *A. manducator* has emerged. Greatly magnified. Original.

Text-fig. 9.—(a) Left mandible of adult. (b) Section through centre of mandible of adult. × 41. Original.

The aperture made in the puparium is usually just large enough to allow the insect to extricate its head and antennæ, thorax and legs, and part of the wings and the base of the abdomen, when by the pressure exerted against the distended abdomen, the voiding of the meconium is assisted, and is either accompanied or followed by a white discharge—the white particles previously referred to,—which instantly dries and has a cement-like appearance. This substance, upon analysis, has been found to contain sodium hydroxide, but whether some of this is used to soften the silk has not been established. The compressed meconium, which is a deep black-brown rod, is completely enclosed in a sac of integument, which resists boiling in caustic potash, giving the impression that it is chitinized and probably the larval mesenteron, which during metamorphosis has become closed at the anterior end and compressed.

In some instances the exit-hole is made too large, and the adult appears with its abdomen still distended; then by constantly passing the tarsi of the hind-legs along it, it exerts sufficient pressure to enable it to void the meconium: this method is not always successful, and results in one or two days in the death of the insect. Flight is impossible with the meconium unvoided, although vain efforts to rise have been observed. In some instances the transverse cut made with the mandibles is extended so far around the puparium that, on emerging, the insect completely breaks off the top of the puparium. Emergence generally takes place from the cephalic end of the puparium, but in several instances it has been observed that this was accomplished from the posterior end.

The wings are always fully extended before the adult attempts to break out of the puparium. Only in a very few cases has it been observed that the wings have become damaged and torn by the jagged edges of the emergence hole; this condition is generally accompanied by injuries to the soft integument between the abdominal plates, resulting in the death of the insect in one to two days.

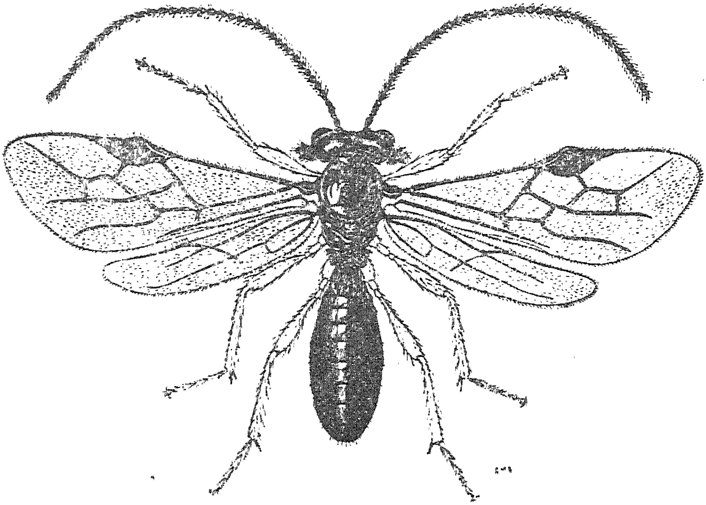
Examination of intact puparia some time after the emergence of the parasites has shown that for some reason unascertained—not due to temperature—a small number never succeed in escaping, whilst a few have been found with the cocoon-lining too thick to extricate themselves.

Nothing of the pupal exuvium of those insects, which void the meconium whilst escaping, can as a rule be seen; it is generally buried under it, whereas the others are usually found with it attached to the apex of the distended abdomen. Males emerge before the females. The greatest emergence of males is from 3 to 4 days earlier than the females.

The Sexes.—Size:—The size of the adults varies considerably, but is, of course, relative to the size of the host. The measurement of several discloses a range of from 2½ mm. to 6½ mm. in length.

General appearance.—The males (text-fig. 10) are easily distinguished from the females by their long antennæ, which are approximately equal to the over-all length of the insect from the frons to the apex of the wings when in repose, and which extend beyond the apex of the abdomen. The ovipositor is barely visible when the insect is looked at from above, but can be seen when in a lateral aspect. Both sexes are shining black, with rufous legs.

Text-figure 10.



Male *A. manducator*. Greatly magnified. Original.

Courting and Mating.—This takes place very shortly after emergence, but never occurs unless the meconium has been voided some time. When seeking a mate (in the cage) the male moves rapidly along, violently swaying the antennæ and vibrating the wings, which are opened as in flight. Mating lasts about 8 minutes, but was not frequently observed. The sex attraction is only evident in the male, and when newly-emerged females were admitted to the cage, males eagerly sought them. The female evinces little interest in the male and can easily repel it. The males make no distinction between virgin and fertilized females.

Flight.—Both sexes are capable of sustained flight. This has been observed in the cage, and on fine days it appeared as if all were "on the wing." Any which escaped from the cages or when handling were generally instantly out of reach and through the open skylights. Those observed around baited receptacles in the open appeared to come from all directions; this is confirmed by Marshall (quoted under *Oviposition*).

Oviposition.—Females do not begin ovipositing until a day or so after emergence, and irrespective of whether they have mated or not; a few have been observed trying to oviposit before voiding the meconium.

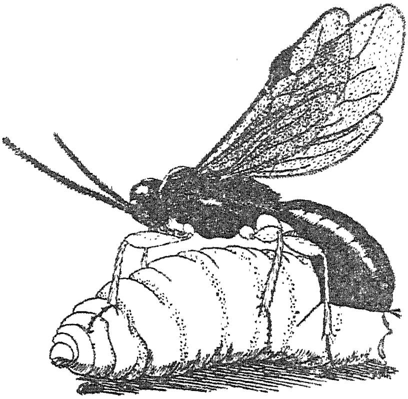
The ovaries are large and well filled with eggs. A dissection of the ovaries of 12 females gave an average of 366 eggs per female. The greatest number counted in a single female was 416. Graham-Smith (4) records a female with ovaries containing "at least 549 eggs." Table II. gives the details of the count of the contents of individual ovaries:—

TABLE II.—Contents of Ovaries of 12 females.

Females.	No. 1.	No. 2.	No. 3.	No. 4.	No. 5.	No. 6.	No. 7.	No. 8.	No. 9.	No. 10.	No. 11.	No. 12.	Total.	Average.
No. of eggs.	412	375	408	368	352	328	363	416	362	325	338	347	4394	366·16

Oviposition takes place in the larva of the blow-fly (text-fig. 11); half- to full-grown larvæ are usually selected. In the cage the chemotropic effect of carrion was—when the atmosphere was not charged with the odour—almost instantaneous upon the females; they became violently agitated, swaying their antennæ, and then might proceed to clean themselves, particularly the antennæ and the abdomen ventrally in the region of the ovipositor, and fly to the carrion, or reverse the procedure and fly over and around the receptacle containing it and the larvæ, and then alighting near by, go through the cleaning process. It is, of course, obvious

Text-figure 11.



Female *A. manducator* ovipositing in larva of *Phormia grænlandica*. Greatly magnified. Original.

that the sense-organs in the antennæ and the palps of the ovipositor had suddenly received the odour of the carrion and stimulated the insect to oviposit. The males are also attracted by carrion—apparently a sexual tropism to enable them to locate the females. Marshall (**3**) observes:—"They" (both sexes) "scent the aroma of carrion at a surprising distance, as I once had occasion to observe in watching the remains of a dead rook, upon which they descended in constant succession, apparently from the sky, like vultures. The males generally alighted on blades of grass close to the attractive object, as if to wait for their partners, without interrupting them in their unsavoury occupation."

As soon as the females have alighted, they begin their search for the larvæ, and if the initial effort to insert the ovipositor is successful, they remain depositing eggs until they die, either from exhaustion or because their task is completed. A few have been observed to leave the larvæ and go in search of food and not return the same day.

Only one egg is deposited in each larva by an individual female, at least, under conditions which are approximately natural—*i. e.*, where the larva has means of escape by disappearing into the meat or earth.

The ovipositor is inserted diagonally under the integument of the larva when the attack takes place in the thoracic or abdominal regions. The larva makes every effort to escape, wriggling and squirming, and frequently damaging the female. These frantic efforts to escape are put an end to by the effect of a poison injected with the insertion of the ovipositor. The immediate effect of the insertion of the ovipositor is to cause the larva to vomit and void. The poison produces a paralyzing effect, and causes the larva to contract and then lie motionless whilst the egg is deposited. This operation varies in time, and may take 30 seconds to 5 minutes*—the more exhausted the female is, the longer it takes.

The "temporary paralysis" of the larva lasts from one to two minutes, so that when an exhausted female delays the withdrawal of the ovipositor the larva endeavours to release itself: normally though, when the ovipositor is withdrawn, it is still motionless, and remains so for some seconds. The female then moves off in search of another victim. The first movements of a larva recovering from the "temporary paralysis" are to extend itself to its full length, and then, still slightly under the influence of the poison and the unpleasant ovipositor, it goes through a series of extraordinary convulsive and constrictive movements, which ripple the integument either from the cephalic to the anal end or vice versa, as though it was endowed with intelligence and was trying to squeeze and crush the egg [*]. As soon as this ceases it hastily disappears into the soil or carrion, apparently stimulated by its experience to pupate. The foregoing observation, naturally, only refers to larvæ free of the carrion or on top of it (otherwise they could not have been observed), but those attacked which are partially buried in it do not appear to behave in the same manner; they are surrounded by food and hidden from the light.

---

* One female, which had not oviposited in more than a dozen larvæ, was observed to retain the ovipositor within a larva for 21 minutes, and as the initial dose of poison did not suffice to keep it motionless, further doses were apparently administered each time it moved. Needless to say, this larva died.

The first 20–30 larvæ attacked will be "paralyzed" instantly, and then the poison apparently becomes less rapid in its effect; whilst it has been noticed that a female which rests for some time and feeds, seems to renew the effectiveness of its poison.

An individual female—as has been already noted—does not normally attack the same larva twice. In this connection a series of experiments were carried out under conditions as nearly natural as was possible, and by employing one female at a time it was observed that each larva parasitized, either free of the carrion or partially embedded in it, made every endeavour to get into the soil after it had recovered from its "temporary paralysis" either directly or through the carrion. It appears to be definite that effective oviposition stimulates the larva to pupate. However, in cases in which two or more females inject the same larva—the second one coming upon it just when it begins to move or encountering it on its way to escape,—its death ensues within 24 to 48 hours. Its organs appear to disintegrate, the dead larva gradually darkens until it turns black; dissections disclosed little else than a thick dirty putrid liquid. In warm weather, with a temperature of about 22° C., the dead larva dries up within 6 or 7 days. The majority of these over-parasitized larvæ never succeed in getting into the soil.

A female does not attack a motionless larva, but may prod it with the ovipositor, usually causing some movement with unpleasant results for the larva. It is also in this way that a larva just recovering from "temporary paralysis" becomes a victim to over-parasitism.

On several occasions the writer has observed a moving larva stop suddenly and lie motionless upon the approach of a female, although it may have been touched by no more than one leg of the latter. This behaviour is obviously due to the larva having been previously attacked by a female, but whether it was attributable to chemotropism, which is most probable, has not been established. The predominant odour was that of carrion.

Females which have been ovipositing for some time and are in a filthy condition from the carrion and putrefactive juices, will endeavour to insert their ovipositor into any object which they happen to feel moving, with the result that frequently two or more can be seen together, "jabbing" their ovipositors amongst each other's legs in a vain effort to get it firmly fixed.

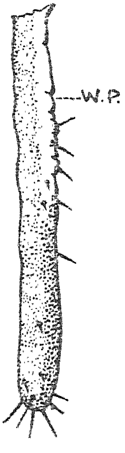
---

[*] The writer, as previously stated, is of the opinion that many of the eggs are damaged by this movement, particularly if located in or amongst muscles.

The ovipositor, which is extruded, is inserted in different parts of the larva's anatomy. Generally, when the larva is free—*i.e.*, on the surface of the carrion, under it, or on the surface of the soil,—it is inserted about the 1st to 3rd abdominal segments; very small females attack the cephalic end or the anal plate, particularly in the case of full-grown larvæ, probably owing to their inability to get astride the victim, as is usual with the larger females. When the larva is moving in the carrion and the movement is perceptible, the female endeavours to insert the ovipositor through it into any part of the larva, whilst a female coming upon a larva disappearing into the soil or carrion will attack the apex of the abdomen or anal plate, and sometimes is unable to bring the victim to a standstill before the ovipositor has disappeared into the cavity; whilst, on the other hand, a larva emerging from the carrion is attacked in the anterior region.

Whilst the insect is ovipositing, the palpi or "feelers" (text-fig. 12), which in repose form lateral sheaths to the poison and

Text-figure 12.



Palp of ovipositor of *A. manducator*. W.P., wiping-pad. × 61. Original.

piercing-blades, are constantly in use for locating the moving larva. The ovipositor is withdrawn from a victim with a distinct jerk in order to disengage the barbs of the piercing-blades, and by means of the powerful muscles attached to the hinge-like continuation of the blades, it instantly springs back between the palpi, the apex of the former alighting at the base of the latter, so that whilst the sternites are assuming their normal position of repose, the point of the ovipositor is cleaned by the "wiping-pads" (text-fig. 12, W.P.) of the receding palpi. These "wiping-pads" are on the inside of the basal portion of the palpi, extending approximately half of the length, and consist of soft dirty white integument roughly in folds.

Length of Period of Oviposition.—Females, whether freshly emerged or otherwise, and which had or had not mated, once allowed to oviposit, were dead the next day if they had been constantly ovipositing, or when resting and feeding occasionally lasted three to four days; in one instance a female lived five days ovipositing in about 50 larvæ daily.

Progeny of Single Females.—No extensive data were obtained on this point, but in the laboratory the average was 33·74 per female. (See *Percentage of Parasitization.*)

Parthenogenesis.—Unmated females reproduced males: whether the latter were fertile was not investigated.

Proportion of the Sexes.—This appears to be about equal on the whole in individual lots of material parasitized in the laboratory, although one sex may considerably predominate. The figures given under this heading are details of emergence from three lots of material which were parasitized by free Braconids in Regent's Park, and give the following result: 199 ♂ and 294 ♀. No other details of emergence from outside material were compiled. Graham-Smith (4) gives, substantially, the following details for "Spring" and "Autumn" batches which emerged in 1916 from material parasitized in the autumn of 1915. The sum total for both batches are 2891 ♂ and 749 ♀, clearly indicating arrhenotokie, a proportion, which the writer ventures to suggest may, in this instance, be due to the immediate proximity of host-infested carcases when the females of the autumn batch of 1915 emerged.

Length of Life of Adult.—In the laboratory the length of the life of adults was not very long. Observations showed that, in the case of two freshly-emerged males which were not permitted to mate, one lived 25 days, the other 31 days; two unfertilized females not allowed to mate or oviposit lived 33 and 38 days; two females and two males confined together, the former not being allowed to oviposit, the males lived, the one 18 days, the other 23 days; the females, one 25 days, the other 33 days. And as stated oviposition rapidly ends the female's life. In each of the foregoing tests ample supplies of food were given, but the insects were confined in glass jars, which did not give much opportunity for flight and the atmosphere was permeated with the odour of carrion. The length of life in the open or in unpolluted air would doubtless be longer.

The length of life within the main cage appeared to be much shorter during the months of November, December, and January in spite of a mean temperature of 20° C. Activity was always greatest on fine days, and particularly when the sunshine was directly upon the cage.

Food.—When the breeding operations began, the adults were fed on sugar diluted with water in a ratio of 1 to 5, but owing to the "Rationing Restrictions," honey had to be substituted, and diluted in the same proportion proved to be the better food, and was occasionally varied with water only. Observation in the open failed to discover any of this species feeding, and in this connection Marshall (3) only observes "both sexes likewise frequent flowers for the purpose of feeding." It is probable that "honeydew" constitutes a source of food, as is the case with many Hymenopterons, but was not tested with this species.

Seasonal Abundance.—From 14th July, 1919, to the end of January 1920, with a few days' exception, there have been active adults in the main cage; the breeding, which, to begin with, was almost a daily occurrence, caused such an overlapping of generations as to bring about this result. Graham-Smith (4) observes:—"The parasite, however, is abundant throughout the season, for it was observed attacking fly larva from 30th May to 1st November, 1916." From the observations of the writer, these insects were present in large numbers from July to October 1919 in Regent's Park; and as the original stock bred in the laboratory appeared on 14th July, and taking the average period of the life-cycle as 52 days (see Table I.), this gives 24th May as the date upon which the parents of this generation were depositing eggs; this therefore confirms the above observation.

Details of Emergence.—Accurate sex details of the daily emergence from certain lots were kept from 18th August to 20th September, after which date these had to be abandoned, the breeding operations at this date occupying all available time. Details of daily emergence for the period 3rd to 12th September, corresponding to the period of greatest activity shown in Table I. and affecting laboratory-bred material from the jars No. 1, No. 2, No. 3, No. 4, No. 5, & No. 6 and from No. 7 for one day shown in Table I., are given below in Table III.:—

TABLE III.—Details of Daily Emergence.

Jars Nos. 1, 2, 3, 4, 5. & 6 and 7 for one day.	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	Totals.
	3	—	3	2	11	3	13	9	17	13	16	38	14	42	17	34	27	31	37	42	*Males.* 158
Dates. Sept.	3rd		4th		5th		6th		7th		8th		9th		10th		11th		12th		*Females.* 214

These figures merely indicate the early appearance of the males. During the period covered by Table III. the average daily contents of the main cage was over 300 individuals of both sexes; this figure allows for the withdrawal of ovipositing females and admission of daily emergences from all sources.

Percentage of Parasitization.—Graham-Smith (1), referring to two lots of material attacked by "free" *A. manducator* in 1914 and bred out in 1915, states:—"In the former it is 60 per cent., in the latter nearly 90 per cent. That the latter figure is a true index of the extent of Braconid infection in the original stock of pupæ is shown by the fact that 9 per cent. of the pupæ in the same tin were not parasitised." Of two lots of puparia from which—the parasite emerged during 1916, this observer found (4):—"At least 25 per cent. of the puparia" from one lot "and 57 per cent. of those" from the other "were infected with *A. manducator*." Summarizing his observations on emergence of this parasite in 1915–16–17, he says (4):—"Of the 16,028 puparia collected in the autumn of 1914–15–16 from sunny and shady situations 7041 or 43 per cent. were infected with *A. manducator*, while of the 4787 puparia collected during the summer months of 1916–17 only 508 or 10 per cent. were infected."

From two lots of material collected from Regent's Park on 27th July, and where parasitization by "free" Braconids occurred under conditions similar to those above, the writer found the percentage of parasitism to be 23·12 per cent. and 52·32 per cent. respectively. These lots were both brought in at a time when the larvæ had begun to pupate, they were examined in November, previous to this time emergence had ceased. The figures given are derived from the number of puparia from which *A. manducator* had emerged, and from those intact puparia in which dead adults, dead pupæ, and active and dead larvæ of the parasite were found, as against the total number of puparia in the receptacles, including those from which flies had emerged, or failed to emerge, and those containing atrophied fly-nymphs. It would be of interest to know the number of females responsible for these figures. Dead females were always found in the receptacle, but no reliance can be placed on their number.

In laboratory-bred material, in ten lots, it was found that the percentage of parasitization ranged from 15·64 per cent. to 48·99 per cent., the latter figure being due to nine females. But the outstanding feature of this examination was, that it took a total of 39 females to reproduce definitely 1306 individuals exclusive of over-parasitized larvæ—an average of 33·74 each, or only 9·89 per cent. of their average egg-capacity. This result can but be attributed to confinement and to the bad ventilation of the cage, also to the fact that the parasite's sense-organs, which are normally stimulated to bring about the inclination to oviposit, would have been dulled and deadened by the ever-present odour of carrion in the laboratory. Under better caging conditions and when living in an atmosphere unpolluted with the stench of the putrefactive juices of the carrion, better results would certainly be obtained.

Hibernation.—*A. manducator* hibernates as a full-grown larva. This was observed under natural conditions by Graham-Smith (**1** and **4**), and is supported by the condition of the stock material and by the Refrigerating Experiment.

Attraction to Light.—Artificial light is very attractive, and caused the insects to crowd on that side of the cage nearest to it.

Hosts.—The species of larvæ used in this work and from which *A. manducator* Panz. was successfully bred, are as follows:—

Lucilia sericata Meig.
,, *cæsar* Linn.
Phormia grœnlandica Ztt.
Calliphora erythrocephala Meig.
,, *vomitoria* Linn.

No preference was shown for any individual species, the odour of the putrefactive juices being the chemotropic stimulation to oviposit; and therefore it is probable that other carrion-feeding cyclorhaphous larvæ would be found to be suitable hosts.

In this connection Marshall (**3**) states:—"They have been reared from various maggots, as *Lucilia cæsar* L., *Cyrtoneura stabulans* Fall., *Hydrotea dentipes* Fab."

LIFE-HISTORY AND HABITS OF *NASONIA BREVICORNIS* ASHM., AND HOSTS.

Historical.—*Nasonia brevicornis* Ashm. was first described by Girault and Saunders, 1909 (**6**). They bred it from the puparia of the Common House-fly (*Musca domestica* Linn.) at the Illinois Entomological Station at Urbana in 1908. It has since been reported from Chili and India, and was bred in 1911 from the puparia of *C. erythrocephala* Mg. by Graham-Smith (**1**) at Cambridge, England. In November 1913 it was bred from the puparia of *Pycnosoma rufifacies* by McCarthy (**2**) at the Government Sheep-fly Experiment Station at Yarrawin in New South Wales, and a few days later discovered at Longreach, Central Queensland (**7**). As already stated, page 197, it was first bred by the writer from the puparia of *C. erythrocephala* collected from Regent's Park, London, in July 1919.

Introductory.—In the following account of the life-history and habits of this insect, the writer freely quotes from the writings of the previous observers, adding here and there observations of his own. In doing this the writer desires to put forward as general and collected an account of this important insect as possible; further, it may be observed that the writer had already made an independent study of this subject before specimens were identified and the original description of Girault and Saunders (**6**) brought to his notice. Full acknowledgment is made to these references, which for the sake of the continuity of the account are mostly signified by reference numbers only.

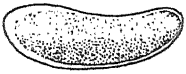
The Length of the Life-cycle.—This is entirely dependent upon the temperature, and its influence affects the full-grown larval stage the most.

The various observers differ as to the period of the life-cycle, but this can be accounted for by the probable differences in temperature when the observations were made. Girault and Saunders (**6**) give 22½ days as the average in the spring and 15 days in autumn; McCarthy (**2**) 11 days in summer; Froggatt

(7) 11 to 14 days; Froggatt (8) 15 days. Under laboratory conditions with a mean temperature of 20° C. it was found to average 21 days.

The Egg.—The egg is translucent white, with a smooth glossy surface, cylindrical, slightly tapering to one extremity and broadly rounded at both ends (text-fig. 13). The newly-deposited egg measures from ·30 to ·35 mm. in length and ·11 to ·14 mm. wide at broadest part (8). The eggs are placed in clusters under the shell of the puparium and upon the surface of the pupal integument of the developing fly, the latter occasionally being punctured by the ovipositor. They are found in clusters of 2 to 12 or more or singly, and are situated on any part of the fly-nymph, but are commonly found in the depression of the junction of head and thorax, or thorax and abdomen. "The eggs appear to be coated with a trace of some sticky substance, which causes them to adhere together, and to the covering integument of the fly-pupæ" (8). The egg undergoes a slight increase in size as the development of the embryo progresses. The duration of the egg-stage varies considerably; those observed ranged from 30 to 74 hours.

Text-figure 13.

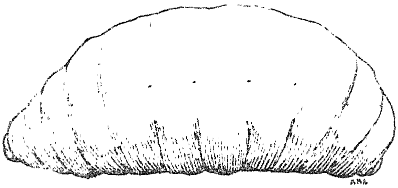


Egg of *N. brevicornis*, 26 hours old. Size ·125×·350 mm. ×41. Original.

The Larva.—Immediately upon hatching, the young larvæ start feeding. They puncture the pupal skin of the host with their mandibles, and with these firmly attached to the enveloping skin of the pupa, proceed to absorb the body-fluids of their host. They remain about the same position until full-grown. As the larvæ develop, the host is gradually absorbed, and consequently shrinks inversely to the growth of larvæ. "As a rule, the remains of a parasitised host—the fully-formed pupa—is a flat, scale-like mass, apparently consisting of the ventral shell of the pupa and that of the head; for example, the thecæ of the eyes, legs, and wings are discernible, and the remains are not much shrunken so far as the original length is concerned. In the case of *Cynomyia cadaverina*, in one puparium infested with 21 larvæ of the first spring generation the parasites were all attached to the dorsal surface of the host from the pronotum to the tip of the abdomen; these parasitic larvæ were nearly full-grown. But in another puparium of the same host, in which 13 larvæ were found, their attachment to the host appeared to be haphazard, and the host-pupa was considerably shrunken, especially in width" (6). No evidence of larval predaceousness is forthcoming, although dead larvæ are frequently found; these are sometimes found with living ones, but usually all are dead. The dead larva is always discoloured and appears to have shrunk to the size of the meconium, so that they are then quite hard.

The number of larval instars have not been worked out, but the general appearance of the larvæ is constant. The larva (text-figure 14) is a typical vermiform hymenopteron, broadest in the centre and tapering towards the extremities. It consists of apparently 14 segments. It has nine consecutive pairs of spiracles, of a very simple structure, on 2nd and 3rd thoracic and 1st to 7th abdominal segments. The integument is smooth, glabrous, very thin and easily damaged; it appears to secrete some sticky fluid which entirely bathes the integument, and which enables it to "grip" the surface over which it is moving. An examination of the larval integument discloses minute pores scattered about the surface and presumably the source of this "sticky" fluid. Larvæ have been frequently found in a puparium from which a number of adults have emerged with portions of pupal exuvia attached, sometimes completely covered with it. The mid-intestine is closed caudally during the entire larval development, and the waste matter within it is brown. This gives the larva a dirty white appearance. The slightest puncture made in an active larva about the centre of its body will cause the contents of the intestine to exude instantly, leaving the larva white. The period of development of the larvæ occupies about 7–10 days from the time of hatching, with a pro-pupal stage of 1–3 days.

Text-figure 14.



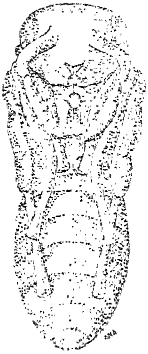
Full-grown larva of *N. brevicornis*. ×25. Original.

A few hours before casting its last larval exuvium, the contents of the mid-intestine is voided. This appears to indicate that the mesenteron and proctodeum become connected before the pupa is formed. "The meconial discharges of this parasite, found scattered through the host puparium, are brownish yellow or dark olive-green in colour, and consist of small conglomerations of round pellets, or are sometimes in irregular chains, like some bacteria, but are never single, solid pieces. . . . ." (**6**).

The length of larval life is very variable.

The Pupa.—After voiding the meconium the larva remains motionless—unless disturbed by a fellow-occupant of the host puparium—with its posterior segments surrounded by the meconial discharge, which dries rapidly. So that when the larval skin bursts and recedes, the pupa (text-fig. 15), which does not entirely free itself from the larval exuvium, consequently becomes anchored to the meconium. This has been observed by emptying the larval contents of a puparium into a small glass tube.

Text-figure 15.



Pupa of *N. brevicornis*. Greatly magnified. Original.

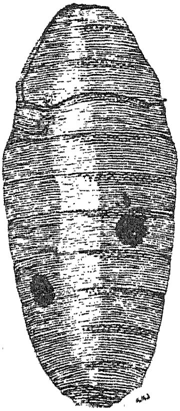
The duration of the pupal stage is variable. "This was obtained in one case only. A larva pupated during the night of Sept. 17–18, 1908, ... The resulting adult female emerged at 10 A.M. Sept. 23, 1908, making a pupal stage of approximately 5½ days. The average length of this stage for the first spring generation (17 cases) was 9 days (May 14–23, 1909)" (**6**). Another observer states:—"The pupal stage occupies about five days" (**8**). Those pupæ observed by the writer ranged from 8–12 days. "When first formed, the pupæ are yellowish white, the eyes garnet, with some duskiness at the caudal edges of the abdominal segments soon afterwards: the mandibles, legs, antennæ, and wing-pads gradually become dusky, and about 48 hours previous to eclosion, the head, thorax, and abdomen, in succession, begin to show dark colour, the head and thorax together becoming a deep black before the abdomen shows very much colour, and then, after about 6 hours, the latter turns gradually but rapidly black. About 20 hours before eclosion the colour is jet-black, which just preceding emergence changes nearly to the colour of the mature adult. At eclosion the adults are fully coloured." (**6**.)

The pupal exuvium, which is very stiff, is a golden brown, and does not recede as in the Braconid, but appears to be broken up in parts; pieces which retain the outline of the antennæ are frequently found loose; similarly, pieces from the head and legs can be found; the abdominal portion seems thinner, and is usually attached to the apex of it when the insect emerges.

The Adult.—Emergence of the Adult.—"In general, it may be stated that the adult parasites emerge from the host puparium through from 1 to 3 circular holes, situated variously, usually in the dorsal or dorso-lateral aspect; and when more than one exit-hole, the two or three are usually scattered or widely separated. The manner of emergence does not differ for sex. The exit-hole varies in diameter from 0·75 to 1·50 mm.; it is usually larger and single when the host is *Musca* or *Chrysomyia* and smaller when *Phormia*, though this difference may be more apparent than real. Individual exit-holes may of course vary considerably in shape; for rarely it may involve the whole of one end of the host puparium, and is then relatively very large and irregular. The margins of the exit-holes are always jagged or serrate, showing that the adults gnaw their way out. . . . . . . In regard to the time of emergence, the males usually emerge from 2 to 20 hours earlier than the females, a few emerging some hours previous to the simultaneous emergence of the majority, but there is considerable variation in individual cases. Thus some males may be the last to emerge, but the tendency is for them to emerge earlier than females." (6.)

In the laboratory the number of exit-holes was not limited to three, four and five have been seen, and the exit-holes, consequently, dorsal, ventral, or lateral (text-fig. 16).

Text-figure 16.



Puparium with two exit-holes latero-ventrally. *N. brevicornis.* Greatly magnified. Original.

Both sexes emerge with the wings fully expanded.

Larvæ have been found in puparia from which—several weeks or months previously—adults had emerged. If this takes place under natural conditions, it would appear that these have very little chance of completing their development, and would probably be killed by mites or some other enemy.

Many attempts were made to observe the initial process of making the exit-hole, but without success. However, on one occasion a female was observed enlarging an exit-hole. A few days previously this particular puparium had been enclosed in a glass tube stopped with a cork. The tube was under observation with the aid of table binoculars to watch the movements of some adults of both sexes which had emerged. There were two exit-holes in the puparium, dorsally, with centres about 3 mm. apart, one being much larger than the other, and through the former all the large females in the tube must necessarily have escaped. Suddenly a female's antennæ were noticed to issue from the small exit-hole, and were violently agitated. The upper part of the epicranium could be seen against the inside of the puparium; the head was then moved, as was evident by the changing positions of the waving antennæ; eventually, after the scapes had several times come into contact with the serrated edges of the exit-hole, they were withdrawn; the female could then be seen changing its position. This accomplished, the head began to appear latero-ventrally through the hole, the right eye coming up first; gradually more and more of the head appeared still maintaining its latero-ventral aspect, until the edge of puparium was slightly oblique to the junction of the mandibles. The right eye and gena were then above the surface of the puparium, the antennæ still inside. The female now began to bite the puparium, the right mandible coming down on it from the outside, the left working up on it from inside. This process continued in a leaf-eating-caterpillar-like movement—semicircular forwards and backwards—until the hole was made large enough to enable the female to escape. No effort was made to test the size of the hole; the insect continued to bite until, suddenly ceasing, it began changing its position again until it was ventral side up inside the puparium, then, moving forward and bending upwards, the antennæ, head, anterior legs, thorax, middle and posterior legs, and abdomen appeared successively, until the female was on the surface of the puparium, erect. It immediately began cleaning itself: the apex of the abdomen bore a portion of the pupal exuvia, which came away with a minute white meconial discharge. A few seconds later the female was found by a male.

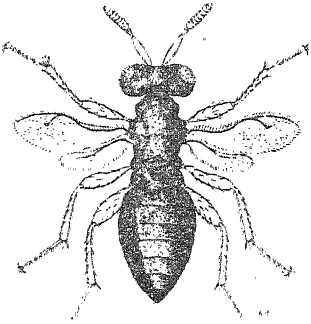
In the laboratory, when the puparia are unburied in soil, these discharges can be seen scattered all over them, and appear as minute white strings.

The Sexes.—Size:—The females vary from 1·0 mm. to 2·30 mm., the males from 0·60 mm. to 2·0 mm. (6).

General appearance.—Both sexes are distinguishable to the naked eye. The females have large wings extending beyond the apex of the abdomen, whereas the males (text-fig. 17) are semi-apterous; their rudimentary wings do not extend farther than the third abdominal segment.

"... the female is a rich dark green, the abdomen nearly black, the head and thorax dorsad, reflecting brassy scintillations, in some lights entirely brassy; in the ventral aspect and also the lateral, the thorax appears bluish; the antennæ dark, the scape and pedicel a rich brown, the legs mostly brown with darker femora. On the contrary, the males appear a brilliant bright metallic green, reflecting brassiness, the antennæ and legs light yellowish brown, the wings small, clouded, with a soiled appearance: the ventral aspect is the same, but with slight traces of metallic bluish. The male is noticeably more brilliant and bright than the female, which is somewhat sombre." (**6.**)

Text-figure 17.



Male *N. brevicornis*. Greatly magnified. Original.

Variations of the foregoing description of the type species were observed in the females; with light brown or yellowish brown femora, not dark or clouded; general colour deep metallic blue: fore-wings not naked in the basal triangle of wings below the submarginal vein, the costal margin with more bristles. Of six such specimens mounted for microscopical examination, no uniformity was found in the venation. The number of setæ in basal area of fore wing varied from 2–5, position also varied. Bristles on costal margin also varied, as many as 14 were observed.

Courting and Mating.—"Courting in this insect is not a complex habit. It follows almost immediately after emergence, at least in confinement. Where a number of both sexes are gathered together, all recently emerged, the males and females are constantly in motion, the former active, seeking the females; the antennæ of both sexes also constantly in motion, held inclined upward in the natural position, giving quick, jerky, wavy movements. When one individual meets another, the antennæ simply touch whichever portion of the body presents itself first, and the two turn aside and pass on; or if they happen to be individuals of opposite sex and (apparently) the occasion is suitable—which is most often the case immediately following emergence—the male hastily climbs upon the back of the female, runs forward, and grasps her head with the fore-feet, usually at the lateral aspect of the eyes or sometimes at the cheeks; the intermediate feet grasp some portion of the thoracic pleura, usually at the mesothorax, and the hind-feet take hold along the sides of the abdomen or the edges of the flat wings. The legs are not stretched out or used for embracing the body of the female, but the hold is taken by the feet alone, and the position of the male is not strained, but rather that of the natural position of rest. His body is parallel with and above the body of the female and projects beyond (cephalad) it, so that the head is between the upturned antennæ of the female and stretched over hers, his abdomen reaching to a point above the third abdominal segment or to a point opposite to the distal end of the marginal vein of the fore-wings, upon which it actually rests. Having quickly attained this position, the male senses the antennæ of the female with his own, and immediately begins suit in earnest by rubbing his head up and down against the inner (mesal) surfaces of the flagella of the female, which are held up in a V-shaped position, at the same time holding the scapes erect and apart and the flagella back, pointing laterad at right angles to the scape and at every downward movement bringing the scapes together; this movement of the head is accompanied by a corresponding "petting" movement of the female flagella against the cheeks of the male. The up and downward movements of the head are regular and continued for from 5 to 10 seconds, each completed movement occupying slightly less than a second of time; and they are alternated with a period during which the head of the male is motionless and his antennæ sensing those of his mate, either by touching both of their tips to the tips of her antennæ, or else by stroking them up and down; the mandibles, maxillæ, and labium with both pairs of palpi are themselves in almost constant motion, but, so far as observed, they play no part as organs of sensation, with the possible exception of the maxillary palpi. Sometimes the male rubs but one of the flagella of the female, turning the head to one side. No other movements than these are observable, but there is some variation in the occurrence of either of the two movements described, and also in the number of times they are repeated before sexual union is permitted by the female. The male may be received coldly; he may make the movements without attempting union, or after alternating them three or four times, he may attempt union without success, and then run forward to repeat the actions, and this may continue as long as the female permits, either resulting successfully or unsuccessfully. In the presence of other females, if received coldly, the male soon tires, leaves and seeks another mate. In order to attempt union, the male has to reverse his position, and run back to the tip of the abdomen of the female, where he usually reaches over the tips of the wings and senses with the antennæ, quickly turning and reaching around again with the tip of his abdomen to gain entrance into the vaginal orifice. Or, on the other hand, he may simply back quickly to the caudal end of the female and attempt union. In one case, ... coition lasted for fourteen seconds, in another for ten seconds. Mating is promiscuous for both sexes." (6.)

During the breeding operations, when females were scarce—being occupied with host puparia,—the writer has frequently observed an unresponsive female crawling about with several males upon her, the lower ones holding on dorsally and laterally, and those above holding on to each other. Sometimes the female with this load on her would try to climb the side of the cage. This effort always ended in the whole party falling to the bottom. On three specific occasions the number of males thus congregated numbered 10, 7, and 11.

The males have some curious habits. When the puparia from which adults have commenced to emerge are lying unburied on soil, a male can be observed to take possession of one, and either stand on it waiting for a newly-emerged female to appear, or he will enter it and periodically make an appearance to seek a mate. Generally the males remain in the immediate vicinity of the puparia from which emergence is taking place, and running over and around these in search of females, they are continually meeting each other; then they start to fight. This usually takes place by means of the antennæ and fore-legs, resulting frequently in the loss of a few joints of the flagella by one or both antagonists. During these scuffles there were sometimes three or four participants, and then it frequently happened that a puparium became dislodged, with comical results if it was occupied by a "domesticated" male: he would sally forth and attack the first within reach: generally one in no way responsible for his discomfort. From a short distance the whole area occupied by the males seemed to consist of combatants.

Females only resorted to fighting when disturbed during oviposition; seldom did males venture into the dishes containing host puparia for parasitization.

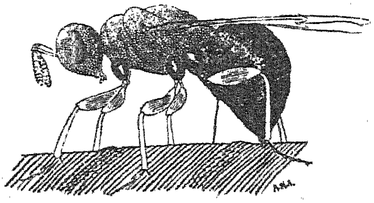
Flight.—The females, in spite of their large wings, are only capable of flying short distances, in a very jerky manner, about 6 feet at a time at most. Before starting on a flight, they usually indulge in a few preliminary movements of their wings. Their most customary method of progress is to crawl.

The males are quite incapable of flight, and the only occasions on which they have been observed to use their wings are when courting and fighting.

Oviposition.—This takes place within a host puparium, preference being shown for those between 24 to 72 hours old—that is to say, after histogenesis has started and the developing fly-nymph is covered in its pupal skin and free of the puparium except where attached anteriorly and posteriorly by the tracheæ. A female will not oviposit in a puparium containing an atrophied fly-nymph, neither one containing a fully-formed fly which for some reason has died or failed to emerge, nor will it oviposit in an empty puparium from which the occupant or occupants have emerged, although efforts to induce some to do so were made by burying that portion from which emergence took place; its behaviour with such puparia is initially the same as with a healthy puparium, but after examination and possibly an attempt to insert the ovipositor, it crawls off in search of others. To enable it to distinguish between those puparia which contain sustenance for its progeny and those which do not, the female must not only possess very delicate sense-organs, but apparently uses the point of the ovipositor, as will be shown later.

Before attempting to insert the ovipositor, a female spends some time critically examining the puparium, crawling over and around it, with her head inclined towards it, constantly waving the antennæ, with which she frequently touches it. Having, apparently, satisfied herself that it is a fit object for attack, she bends the abdomen so that the apex touches the puparium, and then with the tactile hairs upon the palpi and abdomen, and with the point of the ovipositor, she proceeds to prod it until a position is located—such as a groove in the contracted integument of the puparium—through which to make a puncture. The ovipositor is then held in the minute groove, and the apex of the abdomen springs back to a position in which it assumes almost its natural shape, although diagonally opposed to the puparium, and in doing this the full length of the ovipositor is exposed (text-fig. 18); this has hitherto been hidden in its recess along the ventral plates of the abdomen. The female now endeavours to pierce the puparium—not always with success, in which case she moves off to another spot and repeats the process,—which she appears to do with a slight rotatory and up-and-down movement of the ovipositor, accompanied with frequent twitching of the antennæ, a constant movement of the trophi, a slight twitching of the apex of the abdomen, and a general appearance of slight movements as if her entire strength was being exerted upon the task. As the ovipositor gradually disappears into the puparium, the position of

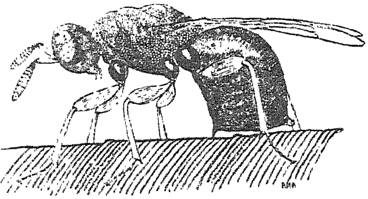
Text-figure 18.



Female N. *brevicornis* ovipositing: 1st position. Greatly magnified. Original.

the hind-legs is sometimes changed, and they are placed further apart so as to lower the body in rhythm. During this movement the abdomen gradually assumes an extraordinary lateral aspect until, when the ovipositor is completely inserted, its appearance is similar to that depicted in text-fig. 19. The flexibility of the sternites is remarkable. Sometimes, after the ovipositor has been inserted its full length, it is partly withdrawn, and appears to be moving slowly in a circle, giving the impression that at this time the eggs are being discharged so as to lie together in a cluster but not on top of each other. Eventually, by lifting the abdomen till it recovers its position as shown in text-fig. 18, and then lifting the thorax with the hind-legs, it disengages the ovipositor, which instantly springs back to its normal hidden position.

Text-figure 19.



Female *N. brevicornis* ovipositing; 2nd position. Greatly magnified. Original.

Generally a minute drop of clear liquid appears at the point of insertion of the ovipositor directly it is withdrawn, but the female moves backwards over the hole until it is located by her palpi or antennæ, and then appears to "suck up" the liquid The drop of liquid is not always visible, and the nature of it has not been determined.

One observer says:—"This liquid is probably used in the first case as a lubricant by bathing the styles as they work on the sheath while puncturing" (**8**). Another:—"The liquid is either a fluid resembling in its nature a synovial fluid, or else it had been acting as a lubricant for the styles; the former is the more probable" (**7**). Another observer says:—"In many cases it (the hole) became covered with a white mycelium-like growth the nature of which we have not determined" (**6**). That the function of the liquid is to seal the hole seems probable. Only in three instances amongst material parasitized in the open have mites (undetermined) been found inside intact puparia inhabited by developing Chalcids, and in one case a pupa had been partially devoured.

The time occupied in ovipositing is variable, ranging from a few seconds to half-an-hour. A few specific instances are quoted:— "The deposition of an egg observed at 9.45 P.M., Sept. 14, required 16 minutes; the host was *Phormia regina*. Another observation made at 10.15 A.M. the same day showed that the act required 8 minutes; the host puparium was that of *Musca domestica*; . . . . A female confined at 9.20 A.M., Sept. 10, deposited into puparia of the *Phormia* at 9.32 A.M. and 1.20 P.M. the same day. One confined at 10 A.M. the same date with two puparia of the same host oviposited at once." (**6.**)

The position of insertion of the ovipositor is very variable. Any segment laterally, dorsally, or ventrally is attacked, in captivity.

One female may insert her ovipositor more than once in the same puparium. One puparium may be attacked by several females in turn; sometimes two will be seen at work at the same time.

Length of Period of Oviposition.—When amply supplied with host puparia, the females appear to live from 3–4 weeks. The first generation from material obtained from Regent's Park were still actively at work, whilst their own progeny were emerging and had begun attacking hosts.

Time elapsing between Emergence and Production.—When host puparia are available, oviposition takes place within a few hours. In three specific instances observed by Girault and Saunders oviposition took place in 24, 10½, and 3 hours after emergence.

Progeny of Single Females.—The number of eggs deposited by a female varies. "In three instances one female placed in a tube with fifteen pupæ parasitized the whole, with the exception of two pupæ which had decayed. The total number developing from the one parasite in the first case was 140, in the second 148, and the third 96. (The numbers emerging from each pupa varied from 15 to 1 in these experiments.)" (**8.**)

In the case of two females each confined separately with host puparia, the first with 130, the second with 86, their respective progeny numbered 21 males, 57 females, total 78, and 38 males, 65 females, total 103. The first female parasitized 17 puparia, the second 22 (**6**).

Parthenogenesis.—"On September 27th, 1908, 12 virgin females of *brevicornis*, reared separately from puparia of *Phormia regina* and in no instance accessible to males, were confined separately, each in a small gelatine capsule with a single known healthy puparium of *Phormia*; on September 29th at 11.30 A.M., in three cases females were observed ovipositing; on October 15th, 1908, the progeny of two of the virgin females emerged as follows:—17 males . . . . and 15 males. . . . . Other emergences did not occur, but in three instances the larvæ of the parasites were found in the host puparia, all dying, however. Hence this parasite is parthenogenetic." (**6.**)

Proportion of the Sexes.—Under this heading Girault and Saunders tabulate the numbers and sexes of 7369 specimens dealt with by them. In lot No. 3 (of this table) they bred 710 males and 786 females; these were from puparia collected "from a single host lot from a decomposed cadaver, city dumpinggrounds." In lot No. 5 they bred 228 males and 116 females from "host puparia in fæcal matter, miscellaneous." These lots represent the most complete figures for material parasitized under natural conditions, and clearly indicate parthenogenetic reproduction.

Length of Life of Adult.—As previously stated, females kept amply supplied with host puparia and a little food lived from 3–4 weeks. The males confined with these females only live 7 or 8 days.

In Australia, under similar conditions and in the cooler weather, they are stated to live from 4 to 6 weeks (7).

When confined in glass cylinders without food or host puparia, they were found to live from 4 to 6 days, the males dying first (6 and 7), and when confined in glass cylinders with food and no host puparia, they were found to live from 18 to 20 days (7).

"The difference in the length of the life of the wasps kept in a confined space, and of those actively at work in the cages, may be due partly to the direct effects of confinement; but in the writer's opinion, it is due more to over-copulation of the females in the confined spaces" (7). This may be partly accountable, but the females appear to be quite capable of resisting the advances of the males, and the writer suggests that the undetermined drop of liquid which sometimes exudes from the punctured puparium, and which all observers agree is generally "sucked up" by the female, may contain nutriment. This would explain why those confined with food and host puparia to deposit eggs in, live longer than those with food and no opportunity to deposit eggs. This view is further supported by the fact that (under breeding conditions) the females seldom left the dishes containing host puparia for food.

It has, however, been ascertained that individuals of both sexes can live for some time with very little food. In the case of three females (presumed to have mated) each was confined separately in tubes within 14 hours of emergence; and into each tube a minute drop of food was placed on the glass by the aid of a needle; no further supply was given. The first female was dead on 15th day, the second on 19th day, the third on the 21st day. Of three males confined separately in tubes (none of them had had an opportunity to mate) and given a similar initial drop of food, one managed to escape on the 7th day through a fissure in the cork, another died on 14th day, and the last on 22nd day. No test was made with virgin females.

Food.—In the laboratory the same food as was used for the braconids and flies was given to these, but very infrequently and only a very little at a time, otherwise they would get stuck in it; and if their wings came in contact with it, they seemed quite incapable of extricating themselves. How the semi-apterous males obtain food under natural conditions is not known; and taking into consideration their habit of remaining in the immediate vicinity whence they emerge, it is very probable that most never obtain any. The females have a better chance with their short jerky flight.

Effective Parasitism.—Under this term Girault and Saunders refer to an interesting phenomenon, and one which was also observed by the writer. It is, that the attack of *Nasonia* can be effective upon the host pupa within 15 to 24 hours prior to the moment when the adult fly would have emerged, the length of the period being approximately such time as is required for the depositing, development, and hatching of the egg, and which in the instances observed by the writer would be from 36 to 74 hours. In a specific instance, and one which must be about the extreme limit of effectiveness, a puparium was noticed to be cracked along the crease at the anterior end, but not sufficiently to have allowed a fly to emerge; it was opened, and found to contain seven larvæ feeding upon a perfect pupal fly which had cracked its enveloping skin anteriorly and the puparium, but which had failed to get any further, its organ of locomotion—the ptilinum—apparently having lost its efficiency gradually as the larvæ fed.

Percentage of Parasitization.—The writer has no figures relative to the percentage of parasitization under natural conditions, and the data relative to laboratory conditions cannot be taken as a true index of the capacity of *Nasonia*, as the number of host puparia presented for attack were worked out on the basis of 20 per female, and the numbers of the latter in the breeding-jars or main cage were only approximately ascertained.

Upon reference to Girault and Saunders the following is found:—"Further, the local abundance of this parasite is indicated by the fact that in at least a portion of the experiment just mentioned, a portion selected at random, the percentage of parasitism was as high as 90 per cent. We have evidence to show, on the other hand, that this percentage of mortality of the host was by no means general, but was considerably lower on the average for this season of the year." (**6.**)

Hibernation.—This parasite hibernates as full-grown larvæ within the puparia of its various hosts. It emerges in the spring, the earliest recorded emergence, in England, being the end of April (**4**).

Attraction to Light.—The females are freely attracted to artificial light, the males very slightly.

Hosts.—The different species of puparia given to *Nasonia brevicornis* to parasitize, and from which it was successfully bred are as follows:—

Musca domestica Linn.
Calliphora erythrocephala Meig.
,, *vomitoria* Linn.
Phormia grœnlandica Ztt.
Lucilia cæsar Linn.
,, *sericata* Meig.

The hosts reported from America by Girault and Saunders (6) are :—

Musca domestica Linn.
Calliphora erythrocephala Meig.
Phormia regina Linn.
Lucilia cæsar Linn.
,, *sericata* Meig.
Chrysomia macellaria Fabr.
Cynomyia cadaverinia Desv.
Sarcophaga species "K" (Spec. nova).

The hosts reported from Australia by Froggatt, jun. (7) are as follows :—

Pycnosoma rufifacies. "Mostly in the field."
,, *varipes.* "To a lesser extent in the field."
Anastellorhina augur.
Pollenia stygia.
Lucilia sericata. } "In the laboratory."
Calliphora erythrocephala.
Sarcophaga aurifrons.

SUPER-PARASITISM, OR ACCIDENTAL SECONDARY PARASITISM.

That *Nasonia brevicornis* might be a "Hyperparasite" upon *Alysia manducator* originally occurred to the writer, when the second lot of puparia were collected from the spot at Regent's Park whence the original Braconid parasitized material was obtained, and when it was found that this Chalcid was emerging from it. However, no Braconid lining to the puparia was observed, at the time, in any from which the Chalcids had emerged: and as the initial breeding operations showed that the latter—then undetermined—bred freely from healthy host puparium, it was assumed that "hyperparasitism" was not the *rôle* of *N. brevicornis*: although it appeared reasonable to suppose that the Chalcid might act accidentally as a secondary parasite in the early stages of development of the Braconid—that is, during the first or second instar—and when the greater part of the fly-nymph still existed. That secondary parasitism in this early stage could take place appears probable; and it does not require a great stretch of imagination to conceive the race for life within a puparium, in the fly-nymph of which an early instar larva of the Braconid is slowly feeding, when suddenly one by one a dozen, more or less, Chalcid larvæ commence feeding operations from the outside of, and through the enveloping integument of the fly-nymph. That the result of such an unequal contest would be against the Braconid, it seems only reasonable to assume; and that the latter would eventually be killed by the Chalcids biting into it. No efforts were made to investigate this point; it appeared too obvious a potentiality, and to search the remnants of a fly-nymph for evidence of the existence of the Braconid of which the chitinized head-capsule of the first instar or mandibles of the second would be the sole initial evidence of its existence, would require time, which the writer at that time could not spare.

Later—in October—a reference was found to this subject, Graham-Smith (1) on pp. 532–4 and on p. 537, in which another Chalcid, *Melittobia acasta* Wlk. (9), is definitely stated to act as a hyper-parasite* on *A. manducator*, and a passing reference to *N. brevicornis* occurs and to the existence of numbers of then undetermined Chalcid larvæ in Braconid-lined puparia. Again, in November, further reference (Graham-Smith) (4) was found to this subject, and this time referring to the presence of *N. brevicornis reared* from puparia with the silk lining of *A. manducator*. This observer states :—" Puparia collected in the autumn of 1916 and kept outside yielded in May 1917 38 males and 36 females. Some of these autumn puparia had been parasitized by *A. manducator*. . . . . Some of these autumn puparia remained intact, and were dissected in March 1918. Of these, 28 were found to contain living Chalcid larvæ, and were kept in tubes in a warm room. Nineteen of these 28 showed infection with *A. manducator*. Adult *N. brevicornis*, 11 males and 48 females, emerged in May 1918, a year and a half after the puparia were collected."

The writer therefore decided to carry out an investigation into this important matter; and as the subject is of considerable interest, the various experiments are given in detail.

To begin with, it might be mentioned that the point previously referred to—*i. e.*, secondary parasitism in the early stages of the Braconid larvæ—was not investigated, for the reason stated.

The following two experiments were made to verify the above quoted statement :—

Experiment No. 1.—A large tube 6 inches × 1 inch was used. Into this was placed—on 25th November—one normal size *Calliphora* puparium, in which a small fracture of the pupal case was made so as to disclose the Braconid lining, and therefore denoting the presence of either a full-grown larva, pro-pupa, or pupa. Three fertilized and recently-emerged females of *N. brevicornis* were then released in the tube, and on the inside of it a small quantity of food was smeared. The tube was kept under occasional observation for four days, during which time none of the females were seen to oviposit, but could be seen crawling over the puparium, carrying out the usual critical examination. After 29th November no further observations were made. On 17th December—21 days later—the tube was opened; the three females were dead, and the puparium was then carefully opened under binoculars. In it was found one active full-grown Chalcid larva, two dead and dried-up larvæ apparently nearly full-grown, and two small shrivelled masses of newly emerged larvæ. The

---

* There appears to have been nothing else in the tins where this occurred except puparia containing individuals of *A. manducator*.

Braconid was found to be in the full-grown larval stage, and was only partially dried up. In endeavouring to move the active larva, the integument was punctured by the needle, and its unvoided waste instantly exuded. This caused the writer to form the opinion that the four dead larvæ of the Chalcid might possibly have met their death by a similar agency—the setæ and sensory hairs (text-fig. 5) on the integument of the full-grown Braconid larva.

Experiment No. 2.—Another examination into this point was therefore carried out. On 30th December four normal-sized puparia, which when fractured disclosed the Braconid lining, were placed separately in glass tubes Nos. 1–4, and into each two fertilized *Nasonia* females were admitted, and a smear of food made on the inside of each tube. They were then corked. On 31st December—the next day—tube No. 3 was found to contain an active *A. manducator* male. The male was released in the Braconid cage, the *Nasonia* females were replaced by new ones, and another puparium—a small one—obtained and put into tube 3. Occasional examination of the tubes was maintained, and, when necessary, fresh smears of food made. On 9th January both females in tube No. 2 were dead. On 10th January, tube No. 1 was found to contain an active *A. manducator* female; the *Nasonia* females were still active. A new puparium was put into the tube, and that from which the Braconid female had emerged was examined. Nothing bearing any resemblance to Chalcid larvæ or eggs was found; the puparium contained the Braconid larval exuvium, pupal exuvium, the meconium, and white cement-like discharge. On 11th February tube No. 4 was found to contain an active female Braconid; both *Nasonia* females were dead. The puparium was examined, and besides its normal contents, two small masses were found adhering to the lining but which were not distinguished. The *Nasonia* females in tubes Nos. 1 and 3 were observed to be dead. On 10th March the contents of tubes 1, 2, and 3 were examined. No. 1 puparium was opened, and found to contain a dead and shrivelled larva of *A. manducator*, and attached to it was a dead Chalcid larva, and loose in the puparium two living Chalcid larvæ. No. 2 puparium contained a dead and shrivelled larva of *A. manducator* with four dried and shrivelled Chalcid larvæ—very small ones—and all adhering to their host. The puparium in No. 3 tube was examined, and towards the cephalic ventral end of it a slit was observed, through which part of the head of an adult Braconid could be seen, as though it had tried to emerge. It was then observed whilst opening the puparium that, at the point where the writer had made a fracture mid-dorsally in the first place, this had either been carelessly done, or the female—for such it was—had extended it in her efforts to emerge when bringing the necessary pressure to bear upon the cephalic end in order to get her mandibles into it, as she would cause the anterior half to bend with her, so that it acted as if hinged, and thus frustrating her efforts to emerge.

No signs of Chalcid infestation was observed. The female may have died within a few days of the start of the experiment.

The foregoing experiments show that, under certain conditions—and with fractured puparia—*Nasonia* can super-parasitize *A. manducator* lined and inhabited puparia, and in two instances three larvæ reached full growth.

Whilst experiment No. 2 was developing, experiments into other directions were undertaken.

It has been previously stated that blow-fly larvæ upon recovering from "temporary paralysis" are stimulated to pupate and to escape from the females of *A. manducator*. It was therefore decided to ascertain to what depth such larvæ worked their way into the soil.

Experiment No. 3.—A wooden box with a sliding lid was requisitioned. One end was removed, and the sliding lid sawn across into strips an inch wide. Thus when placed upright with the remaining end as the base of the box, the original base formed one side and the sliding lid in strips the other, with the original sides as ends.

This box was then gradually filled with soil which, during the building up of the requisite depth, was twice subjected to running water to damp it. Seven inches of soil were eventually put in. On the same day—9th January, 1920—pieces of liver upon which fly-larvæ had been feeding were placed on the surface of the soil in a compact mass. One female *A. manducator* was then caught in a tube from the main cage. The mouth of the tube was then held over the liver until the female was stimulated to descend upon it. As soon as she got on to it, she started examining it for larvæ. 25 of these, about three-quarters to full grown, were at hand; they were placed near the female, one at a time, so soon as she had oviposited into each of them. In three instances she attacked twice, having failed to come in contact with the substitutes, and in each case the latter were withdrawn and given to her a second time. It took 57 minutes to get the 25 larvæ parasitized. The female was moved back into the tube and given a smear of food on the cork. She was allowed to rest in the tube for 20 minutes. In the meanwhile another 25 larvæ had been collected. The female was now released again, and the same process started, but she only attacked one of these larvæ; and although others were placed near her, she could not be induced to attack any more, and after 26 minutes the experiment was given up for the day. The remaining 24 larvæ of the second lot were returned to their breeding dish, and the female caught and left in the tube with food.

No further action was taken for the next two days. On 12th January, 1920, the experiment was continued. The above female was found dying; another was therefore removed from the cage, and at 2.30 P.M. it was set to work on 25 larvæ as before, but at 3.25 P.M. it suddenly became dark, and the female refused to oviposit any more. In this time—55 minutes—she had dealt with

20 larvæ. The remainder, five, were returned to their dish, and the female placed in a tube. The surface of soil was on this date quite dry.

On 14th January the contents of the box were examined, but in removing the first inch strip of the "side," some of the dry soil fell out and the dead larva with it (this is recorded as $\frac{1}{2}''$ in the table); greater care was then exercised in removing the other strips. The result is shown for convenience in Table IV.

TABLE IV.—Depth of Soil penetrated by parasitized larvæ.

Depths	$\frac{1}{4}''$	$\frac{1}{2}''$	1″	$1\frac{1}{4}''$	$1\frac{1}{2}''$	$1\frac{3}{4}''$	2″	$2\frac{1}{4}''$	$2\frac{1}{2}''$	$2\frac{3}{4}''$	3″	Totals.
Larvæ	—	1*	—	—	3†	—	1	2	—	—	—	7
Puparia	—		1	1	3	4	6	7	10	3	4	39
Totals	—	1	1	1	6	4	7	9	10	3	4	46

* Dead. † 1 dead.

When removing the soil, which was done by gradually scraping it off with the edge of a steel rule, it was found that at $2\frac{3}{4}$ inches down the soil was caked and still damp. This coagulation was no doubt due to running the water into the box on very dry soil. Seven of the puparia were broken in scraping the soil off.

Experiment No. 4.—Another experiment of the above description was carried out, but in this instance the soil was spread out into a tray and damped before putting it into the box. The same wooden box was used, and filled with this soil to a depth of 7 inches. The experiment was started in the morning of 22nd January, 1920. Pieces of liver were placed on the soil, and one female *A. manducator* allowed to emerge from a tube on to it; 25 larvæ were then given separately for oviposition. The female effectively dealt with these in 45 minutes; she was then removed and another female taken from the cage. The second female was also given 25 larvæ, and disposed of these in an hour and a quarter. Over-parasitization was observed to take place in one larva in this experiment.

On 27th January, 1920, five days later, the contents of the box were examined by the same process of scraping the soil off; it had not coagulated in this case, and only two puparia were broken. The result of the experiment is given in Table V.

Table V. shows that 19 larvæ went deeper than any in No. 3 experiment, there being an absence of caked soil.

Both experiments Nos. 3 and 4 showed that the majority of Braconid parasitized larvæ reached 2 inches or more under the surface of the soil.

Three experiments were made to ascertain the burrowing capacity of *N. brevicornis*. Nos. 5 and 6 were started before the

TABLE V.—Depth of Soil penetrated by parasitized larvæ.

Depth ..	¼"	½"	¾"	1"	1¼"	1½"	1¾"	2"	2¼"	2½"	2¾"	3"	3¼"	3½"	3¾"	4"	4¼"	Totals.
Larvæ ..	—	—	3*	3†	—	1	—	1	—	—	1	1	—	1	—	—	—	11
Puparia ...	—	—	—	—	—	—	3	2	4	5	4	3	4	7	4	2	1	39
Totals	—	—	3	3	—	1	3	3	4	5	5	4	4	8	4	2	1	50

* 2 dead. † 2 dead.

writer was in possession of the information gained in experiments Nos. 3 and 4.

Experiment No. 5.—A cylindrical glass jar was used. It was filled with 5 inches of damped soil; on this was placed a piece of liver with some larvæ feeding upon it. They were mostly full grown. This experiment was started on 20th December, 1919. On 22nd December it appeared that the larvæ had ceased feeding and had gone into the soil to pupate. The liver was therefore removed, and under it two puparia were found; no others were visible. The liver was replaced. 18 fertilized females of *Nasonia brevicornis* were then released in the jar, which was at once covered with bolting silk, and this smeared with food. On 1st January, 1920, adult *C. erythrocephala* were emerging; no Chalcids could be seen, so no further supplies of food were given. The flies were left to die, so that nothing should be disturbed. Adults continued to emerge up to 5th January; a few days later they were all dead. On 10th January, as no living adults could be seen, neither flies nor parasites, the two puparia on the surface were removed, and the contents of the jar emptied and sorted. No attempt was made to gauge the depth to which the larvæ had crawled. The jar was found to contain 47 empty puparia and an equal number of dead flies. 14 intact puparia were found; these were opened, and yielded four puparia containing Chalcid larvæ; the remainder consisted of dead fully-formed flies or atrophied fly-nymphs with no sign of Chalcids. The two puparia from the surface were filled with Chalcid larvæ. Of the Chalcid females, only 15 were collected; the other three were not searched for a second time in the soil.

Experiment No. 6.—This was another burrowing test, in which 20 puparia were placed at various depths ranging from two at 5 inches to seven on the surface, and were situated near the glass side so as to be visible to the observer. The soil used was very dry and lumpy, with a certain amount of fine dust due to the crumpling of the lumps. Four females and one male were released in the jar. Mating was observed. The experiment started on 1st January 1920; and on 20th February, when the contents were emptied and the intact puparia opened—there were only four of these, flies had emerged from the rest,—none bore any signs of Chalcids. This experiment, therefore, was a complete failure. The only point of interest was that the two flies placed at a depth of 5 inches reached the surface.

Experiment No. 7.—This was also a burrowing test. It was started on 30th January, 1920. The same jar was used as in No. 4. It was filled with 2 inches of damped soil, and on this 93 newly formed puparia were placed; above the puparia 2 inches of damped soil was run in. (The writer was now in possession of details of tests 1 and 2.) On the surface of the soil 12 more puparia were scattered, and a piece of liver upon which larvæ had been feeding was also put in. The liver covered five of the surface puparia. The liver was used to reproduce, on a small scale, natural conditions. 20 fertilized females were released in the jar on the same day; it was covered with bolting silk and smeared with food. The jar was kept under observation. From 31st January to 9th February some of the females could be seen at work on the surface puparia. From 10th February to 13th they appeared to be dying. On the latter date *C. erythrocephala* began to emerge, and continued to do so for several days. On 18th February all flies were dead. On 19th February the contents were examined. The 12 surface puparia were opened, and all found to contain Chalcids in advanced or early pupal stage, and a few as larvæ. 72 dead *Calliphora* were found on the surface. The 93 puparia at a depth of 2 inches below surface were then turned out, and 72 empty puparia were found; the remainder, 21, were still intact, and were opened and examined. No signs of the Chalcids were found; the contents of these intact puparia were dead flies in various stages and atrophied nymphs.

Experiments Nos. 4 and 6 indicate that female *Nasonia*, even when confined in a small space with host puparia covered with soil loosely run in, are incapable of burrowing to any extent; and in this connection the following observation of Froggatt (7) is quoted:—"It is generally amongst the pupæ of *Pycnosoma rufifacies*, and to a lesser extent *P. varipes*, that this species of Chalcid wasp is found actually at work in the field. This is largely due to the habits of the larvæ of these two species, which do not crawl away from a carcase to pupate unless the remains have been much disturbed, but pupate either just under the edge of the remains or else affix themselves to the bones, wool, or other portions of the carcase, and thus they are more easily found than the other species, all of which generally crawl a considerable distance from the carcase, and scatter . . . . . . No definite reason can yet be assigned to the apparent distaste of the wasps for the pupæ of *Ophyra nigra* and *Pycnosoma varipes* in the laboratory. In the field the pupæ of the latter species are practically always found to be parasitized."

Further, *Nasonia* does not bear the appearance of a burrowing insect; its head, viewed dorsally, is wider than any other part of its body, whereas *Melittobia acasta* females (specimens of which Mr. Waterston kindly gave the writer) have a narrow head sloping backwards ventrally, and which is attached to a tapering thorax, narrowest at the back of the head, and certainly better adapted for burrowing in loose soil.

The last point investigated was an examination of all the puparia contained in two jars, of parasitized material obtained in the open. The contents of these jars, it should be explained, were the result of exposing meat on soil in a glass receptacle at the Society's Gardens, with the object of obtaining additional supplies of the Braconid. The collection of the contents of this receptacle was delayed until 14th August, and when sorting out the intact puparia from those from which blow-flies had emerged, the writer came across a few dead female *Nasonia* as well as dead female *A. manducator*. It was therefore assumed that a double infestation had taken place. At the time, an attempt was made to differentiate between the puparium of one or other of the parasites, but both were in too early a stage to disclose any difference when subjected to transmitted light. The material was consequently left unsorted, and emptied into two jars to await developments. *Nasonia* began to emerge on 31st August, and in order to give these an opportunity of escaping as they emerged, the linen covers of the jars were replaced by pieces of mosquito netting, through the mesh of which the females were able to escape. Both jars were placed inside a large glass cylinder. This was used as the cage, and in it were put dishes with supplies of blow-fly puparia for the Chalcids. On 3rd September *A. manducator* began to emerge; the Chalcids were still doing so. This continued until 29th September. This state of affairs necessitated constant handling of the jars to release the Braconids, so that the contents became disturbed; and although it was not observed at the time, it now transpires that some of the *Nasonia* females never left the jars, but proceeded to super-parasitize the Braconids in their puparia, and, further, some of those—the progenitors of the above—found dead in the receptacle when the material was collected probably did the same.

When all the puparia had been collected from the jars, they were sorted under three headings:—(A) Those from which *A. manducator* had emerged, (B) those from which *Nasonia* had emerged, and (C) those which were intact. Those from which blowflies had emerged had already been removed, and the number is not known. The numbers under the three headings were:—(A) 195, (B) 50, (C) 506. Those under (A) were put aside, those under (B) were dissected for evidence of successful super-parasitism, and those under (C) were dissected and classified under several headings as follows:—

(1) Atrophied fly-nymphs. (2) Dead fully-formed flies. (3) ,, Braconid larvæ. (4) ,, ,, pupæ. (5) ,, ,, adults. (6) Active ,, larvæ.	No signs of Chalcid attack.

(7) Unlined puparia, with active Chalcid larvæ. (These had, superficially, fly-remains.)

(8) Braconid lined puparia, with dead Chalcid larvæ. (The Braconids were in all stages, pupæ predominating.)

(9) Braconid lined puparia, with active Chalcid larvæ. (These Braconids were in all stages, pupæ predominating.)

(10) Braconid lined puparia, with some dead Chalcid imagines and larvæ. (These consisted, with one exception, of at least one male.)

The examination of these puparia showed that where super-parasitism had taken place, with the exception of a very few instances—the numbers were not noted,—the puparium concerned was a very small one, about the size of *M. domestica*, and consequently, in the case of a blow-fly, a puparium with an exceptionally thin integument. And, further, that the attack of the Chalcid larvæ had taken place in the abdomen of the Braconid where this was an advanced pupa, the only part where soft integument exists, due to the distention of the abdomen consequent upon the presence of the meconium (text-fig. 7): it, therefore, seems conclusive that a *Nasonia* female is able to distinguish between a hard surface and one yielding to pressure, by means of the apex of her ovipositor. It is worthy to note that *Nasonia* appeared to be most effective when the Braconid was a pupa—that is to say, in the identical stage of development to that of its normal dipterous hosts.

The numbers under the heading (B) were (1) 33 puparia, with Chalcid exit-holes and unlined by the Braconid, presumed primary parasitism; and (2) 17 with Chalcid exit-holes and definite super-parasitism. In each instance the puparium had been lined by the Braconid. A feature of these 17 puparia was the position of the exit-hole: in 3 it was made in or about the middle of the puparium, in 6 at the apex of the anterior end, and in 8 at the apex of the posterior end. In only one instance had two efforts been made to escape. This occurred in one of the 3; a small somewhat elongated aperture had been made in a position diametrically opposed to the exit-hole used. A point of great interest in the writer's opinion, with regard to the position of the exit-hole in the above, is that in 6 the Chalcid got out at a point where the Braconid lining is weakest—that is, where it is run over the protruding chitinized mouth-parts of the late blow-fly larva; and in 8 the Chalcid got out at the next weakest point—that is, where the lining is run over the blow-fly larva's posterior spiracles.

The figures under heading (C) are not given in detail; those for sub-headings (1) to (7) do not materially bear on the subject of the investigation, but for 1 and 2 they were very high, and mainly due, in the writer's opinion, to the unshaded position of the glass receptacle and consequent evaporation of any moisture in the soil, which was aided by the delay in removing the contents. Whereas the figures for (8), (9), and (10) do bear on the subject; they are as follows:—

(8)	69	Braconid	lined	puparia,	with dead Chalcid larvæ.
(9)	15	,,	,,	,,	with active* Chalcid larvæ.
(10)	23	,,	,,	,,	with some dead Chalcid imagines and larvæ.

The outstanding point in this instance of super-parasitism is that most of it did not take place in the open, so far as (B) (2) and (C) (8), (9), and (10) are concerned; it actually took place in the jars in the laboratory, and in proof of this postulation, the puparia could not have been lined by the full-grown larvæ by 14th August, or the adults would have emerged before the 3rd September, and further super-parasitized Braconids would have been in the larval stage if it had taken place in the open, whereas the contrary was the case.

To conclude: it has been shown in experiments Nos. 1 and 2 that under certain circumstances *Nasonia* is capable of super-parasitizing a Braconid larva within its lined puparium; and in experiments Nos. 3 and 4 that blow-fly larvæ attacked by the Braconid are stimulated to escape and pupate, and that the majority of them—76 per cent.—reached 2 inches and more below the surface of the soil; and in experiment No. 5 *Nasonia* was unable to burrow to the depths reached by the majority, 93 per cent. of the unparasitized blow-fly larvæ; and in experiment No. 7 definitely failed to reach any one of 93 puparia 2 inches under the surface, which is consistent with their behaviour in the field.

And, it must be pointed out, that in each instance of super-parasitism reported by Graham-Smith (**1** and **4**) it appears that the puparia—subsequently ascertained to contain the Braconid primarily—were collected and moved from a "sun" tin to a "shade" tin or vice versa; and in the case reported by the writer, emerging *Nasonia* remained in the jars containing Braconid parasitized puparia, which were no doubt dislodged by the frequent handling of the jars when releasing Braconids. So that in none of these instances were the conditions even approaching natural.

It therefore appears that if super-parasitism takes place in nature, it is not very frequent and then only accidental, and that where it does take place in a puparium of a full-grown blow-fly larva which has been reinforced by a normal Braconid lining, it is doubtful whether the small, short, and rectangular mandibles (text-fig. 20, *a*, *b*, *c*) of *Nasonia* will enable it to escape; whilst in the case of the female *Melittobia acasta*, this is aided by the distinctly acute mandible (text-fig. 20, *d*) with its one large outer tooth.

---

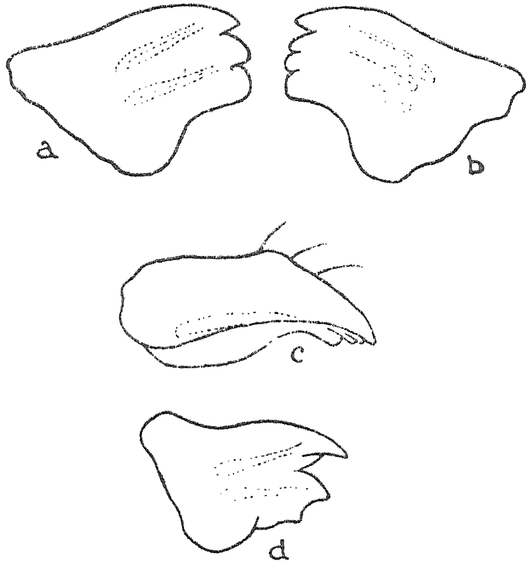
* A few of these were found singly in the puparia, and are the largest *Nasonia* larvæ seen by the writer.

Refrigerating Experiment.

In order to ascertain if the parasites would be able to undergo six weeks—the length of sea voyage to Melbourne—in the refrigerator of a ship, a few of the parasites etc. were given a test.

Prof. Blackman was approached, and kindly gave the writer permission to use a small cupboard in a refrigerating machine in his department.

Text-figure 20.



Mandibles of *Nasonia brevicornis* male: (a) left; (b) right; (c) right, in profile, outer tooth on top. × 160. Original. (d) Mandible of female *Melittobia acasta*; only females of this species emerge. After Waterston. (d) is not proportionate with (a), (b), and (c).

As other experiments were going on at the time, it was necessary to use a burying medium in which no insect life existed, and clean sand was therefore used.

A large glass jar was used as the receptacle, and sand to a depth of 3 inches was run into it as a foundation. A few puparia containing *A. manducator*, *N. brevicornis*, *Calliphora erythrocephala*, and a few larvæ of the latter species were each buried in sand in separate glass tubes left open; these were then pushed into the 3-inch foundation of sand to keep them vertical.

The jar and contents were put into the chamber on 28th November. The constant temperature was reputed to be 2° C. On 15th January—6 weeks and 6 days later—the jar was removed to the laboratory and the contents examined.

One Braconid, a male, had emerged, on what date is unknown;

another Braconid puparium was found with a dead adult half-way out of it, the remainder were intact; one of these was opened and found to contain a living Braconid larva. The Chalcid-infested puparia were all intact; one was opened and contained living larvæ. The *Calliphora* puparia were intact, and as the outline of advanced fly-pupa could be seen in each, they were left so; the *Calliphora* larvæ were all dead. The contents, except the latter, were returned to the jar in their respective tubes, and it was placed about 3 feet from a Bunsen burner. On 16th January one female *Calliphora* emerged, and in the next four days all had emerged. The Chalcids commenced emerging on 30th January, and continued to do so for some days. The balance of the Braconids began to emerge on 12th February.

To summarize: both parasites were able to stand the test when put into the refrigerator in their respective full-grown larval stage—that is, the customary hibernating condition.

CONCLUSIONS UPON THE ECONOMIC IMPORTANCE OF *ALYSIA MANDUCATOR* PANZ. AND *NASONIA BREVICORNIS* ASHM.

It is obvious that, in discussing this subject, the writer is only able to treat of it from a theoretical standpoint. But in doing so he is influenced by a desire to place on record some opinions which have been formed during the course of this work, and some of which gain considerable support from the observations and writings of those who have dealt with these parasites before him.

It would appear that both parasites working in conjunction would form an excellent combination, the one attacking the larval stage, the other the pupal. And between them—it may be assumed—a beneficial influence would be exerted in the control of the Blow-fly.

The occasional and accidental super-parasitism on the part of *N. brevicornis* is but an assurance of the maintenance of the "Wave Law"*. It is actually a twofold assurance, because although *Nasonia* may kill the Braconid, it may itself die in the course of development or become entrapped—upon reaching the imaginal stage—within the silk-lined puparium of the blow-fly larva.

Individually, *Alysia manducator* is considerably superior to *Nasonia brevicornis* as an enemy of the Blow-fly. The former is vastly superior in flight—in both sexes—a most important factor where artificial distribution is concerned; and it is also so from the greater number of hosts it can injure and eliminate in the course of breeding; the ratio is approximately 40 : 1. Its egg capacity is nearly four times greater than the Chalcid, and equal to and in some cases greater than that of several species of blow-flies. In length of imaginal life it is about equal to the Chalcid; the period of development from egg to imago is longer, and in individuals of the same parent a considerable variation takes place, but where artificially propagated, this would be a great advantage in ensuring a continual overlapping of generations, and so obtain the benefit of its activity throughout its season.

---

* Pointed out to the writer by Prof. Lefroy.

On the other hand, the females only of *N. brevicornis* are capable of flight, and which—so far as has been observed—consists of long jumps of 6 feet or so at a time, its commonest method of progression being to crawl. The males are semi-apterous and quite incapable of flight, and although they are of a domesticated "temperament," remaining in the vicinity whence they emerge, they are very liable to overlook their natural functions whilst endeavouring to obtain mastery over rivals, and consequently the unfertilized females would, parthenogenetically, produce a colony of males, possibly isolated and incapable of finding mates or doing any damage to blow-flies. For these reasons, it seems obvious that *Nasonia* cannot prove to be a decisive factor in blow-fly control unless they are constantly distributed in large numbers over small areas. Whereas, if they were artificially propagated and distributed on these constant refuse-heaps found in and around populous areas, and near dung-heaps in town and country stables—whence to be farther, unwittingly, distributed,—*Nasonia* would, on account of its semi-social and "domesticated" habits, prove a most important factor in the control of "The Common House-or Typhoid-fly and its allies," which are constantly breeding in such stercoraceous places and where host puparia would be within crawling distance of the Chalcid.

SUMMARY.

(1) The breeding operations and accumulation of supplies of *Alysia manducator* Panz. and *Nasonia brevicornis* Ashm. commenced in July and ceased in December 1919.

(2) *Alysia manducator* oviposits in the larvæ of several carrion-feeding Diptera. Only one parasite emerges from each host puparia. Over-parasitism kills the larva. The mean average of the life-cycle is 52 days, and as short as 25. Both sexes are capable of sustained flight, and lived over a month in captivity. Average percentage of parasitism over three years was 43 per cent., observed by Graham-Smith (4). Average contents of ovaries 366 eggs for 12 females.

(3) *Nasonia brevicornis* oviposits in the puparia of several species of stercoral and carrion-feeding Dipterous larvæ. From one to 62 individuals have been found in single puparia parasitized in captivity. The length of the life-cycle ranges from 11 to 22½ days in different countries. Only the female can fly, and then only very short distances, and can live, whilst ovipositing, from 4 to 6 weeks, but for a considerably less period without host puparia. The male remains near the vicinity of emergence, where its life is spent in fighting and mating. Average progeny in the case of five females—observed by Girault & Saunders and McCarthy—was 113 per female, and affecting on the average only 16·4 hosts.

(4) *Nasonia* can act as an accidental secondary parasite upon *A. manducator* if and when puparia containing the latter are within its limited reach.

(5) Both parasites in their hibernating stage—*i. e.*, full-grown larvæ—can successfully withstand over 6 weeks at 2° C.

(6) *Alysia manducator* appears to be a more important parasite as a natural control for the Blow-fly than *Nasonia brevicornis*, which appears to be more effective as a natural control of Diptera which constantly breed in permanent refuse- and garbage-heaps, and where hosts would be within crawling distance, such as primarily the Common House-fly, *Musca domestica*.

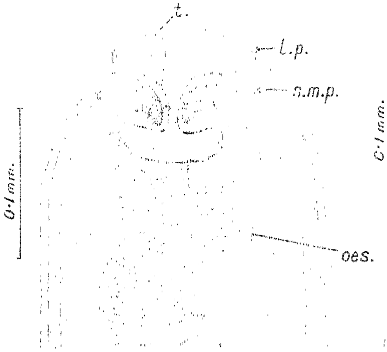
ACKNOWLEDGMENTS.

To Miss Cheesman, Curator of the Insect House of the Society's Gardens, Regent's Park, the writer is indebted for the original lots of material from which the parasites emerged, and for her assistance in procuring additional supplies of both blowflies and parasites.

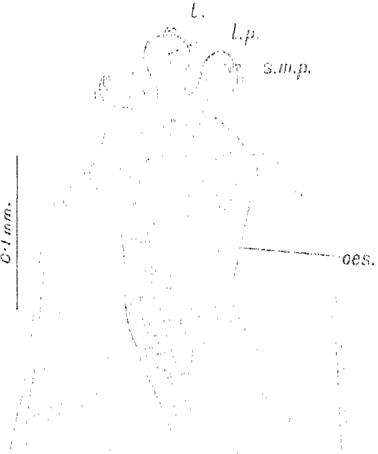
To Mr. J. Waterston, Natural History Museum, the writer's thanks are due for identifying the parasites. Acknowledgments are also due to Mr. C. Gunns, Head Laboratory Assistant at the Imperial College (Zoology Dept.) for assistance in maintaining supplies of cages, breeding and feeding materials.

REFERENCES.

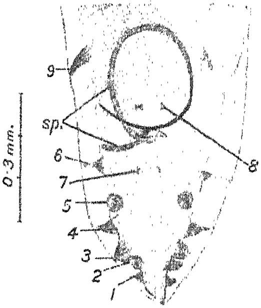
1. GRAHAM-SMITH, G. S.—"Observations on the Habits and Parasites of Common Flies." Parasitology, June 1916.
2. FROGGATT, W. W.—Miscellaneous Publication No. 1716. "The Sheep Maggot-fly (*Calliphora rufifacies*) and its Parasite." Agricultural Gazette of New South Wales, Feb. 2, 1914.
3. MARSHALL, Rev. T. A.—"A Monograph of British Braconidæ," Part V. The Transactions of the Entomological Society of London, 1894.
4. GRAHAM-SMITH, G. S.—"Further Observations on the Habits and Parasites of Common Flies." Parasitology, Oct. 1919.
5. GATENBY, J. BRONTÉ.—"Notes on the Bionomics, Embryology, and Anatomy of Certain Hymenoptera Parasitica." Journal of the Linnean Society, No. 224, June 30, 1919.
6. GIRAULT, A. A., and SAUNDERS, G. E.—"The Chalcidoid Parasites of the Common House- or Typhoid-fly (*Musca domestica* Linn.) and its Allies." Psyche, Dec. 1909 and Feb. 1910.
7. FROGGATT, J. L.—"An Economic Study of *Nasonia brevicornis*, a Hymenopterous Parasite of Muscid Diptera." Bull. Ent. Research, March 1919.
8. FROGGATT (1915).—Extracted by Graham-Smith, G. S. (1).
9. WATERSTON, J.—"Notes on the Morphology of Chalcidoidea bred from *Calliphora*." Parasitology, vol. ix. No. 2, Feb. 26, 1917.



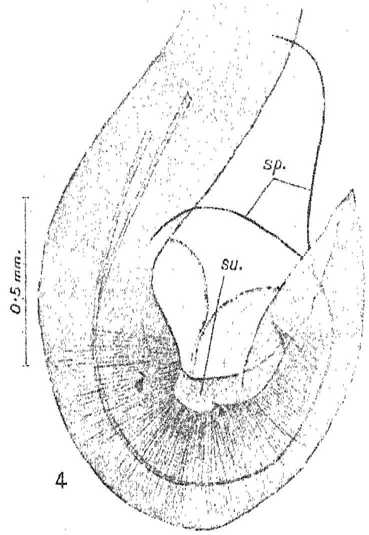
1



2



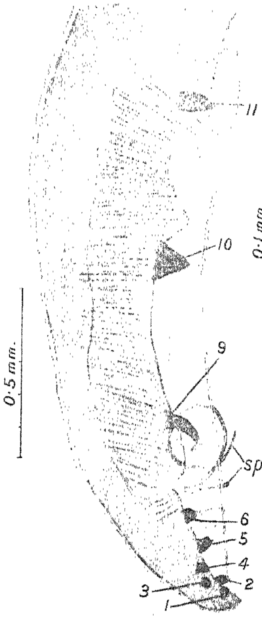
3



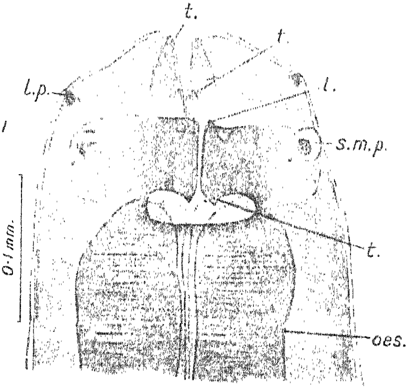
4

Bale & Danielsson, Ltd

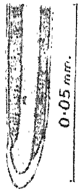
GNATHOSTOMIDÆ.



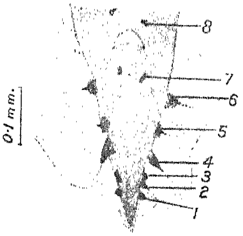
5



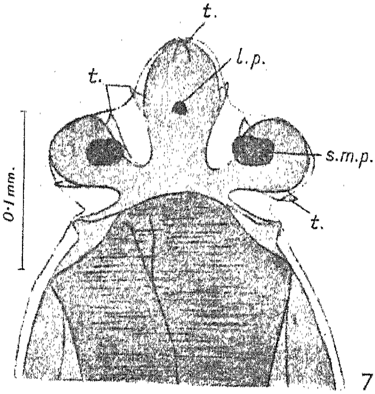
6



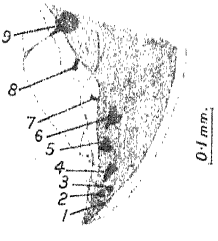
10



8



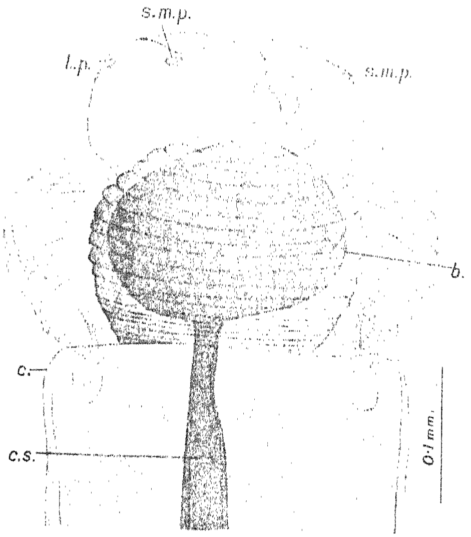
7



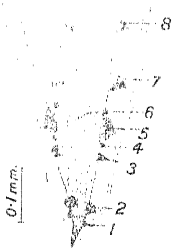
9

Bale & Danielsson, L^td

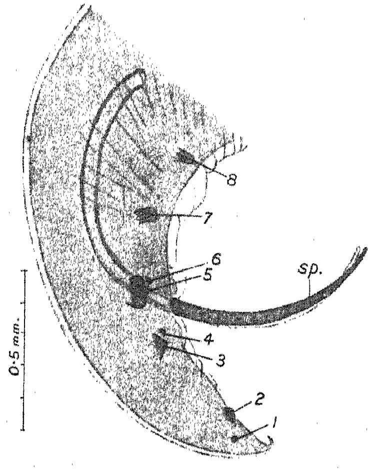
GNATHOSTOMIDÆ.



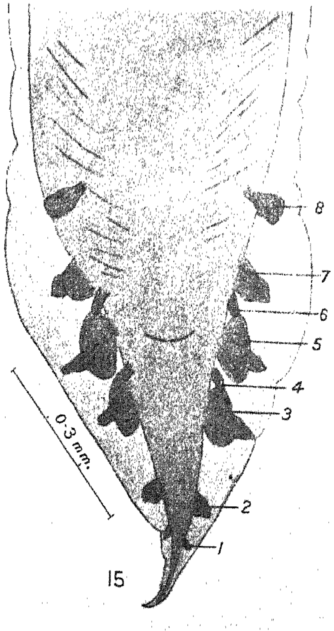
11



12



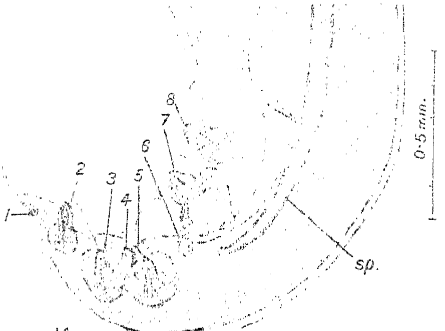
13



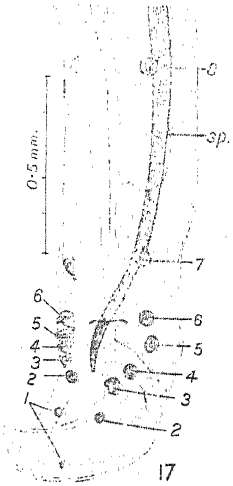
15

Bale & Danielsson, Ltd

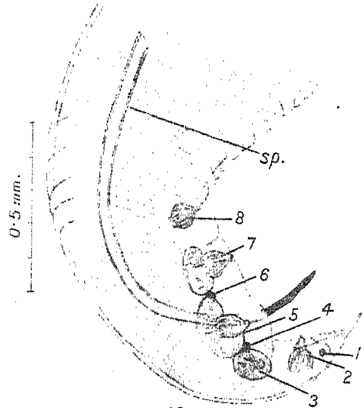
GNATHOSTOMIDÆ.



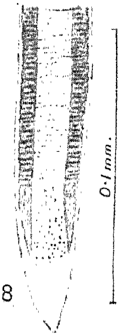
14



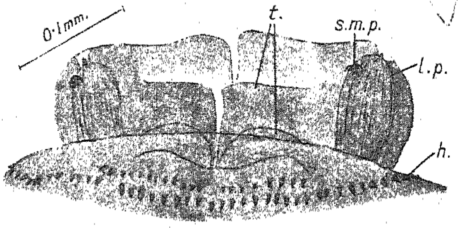
17



16



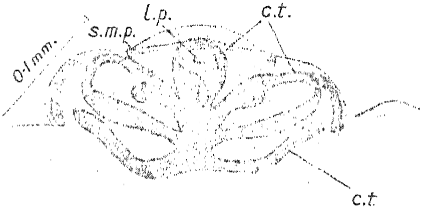
18



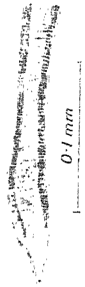
19

Bale & Danielsson, Ltd

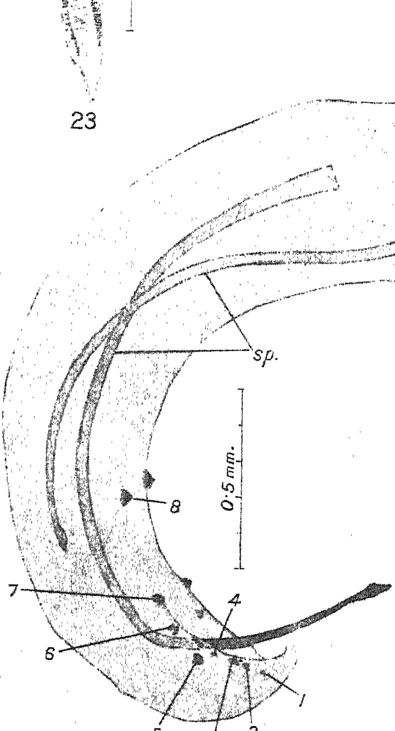
GNATHOSTOMIDÆ



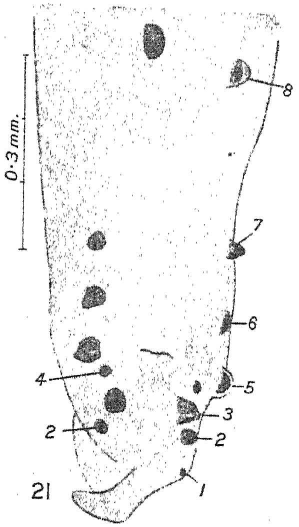
20



23



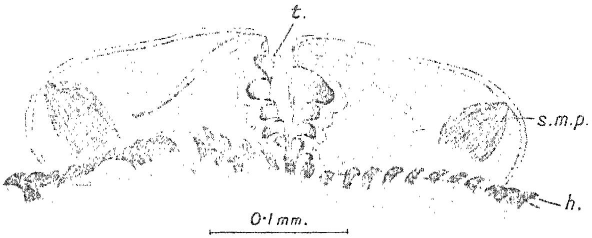
22



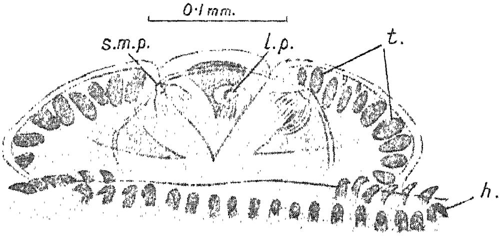
21

Bale & Danielsson, Lᵗᵈ

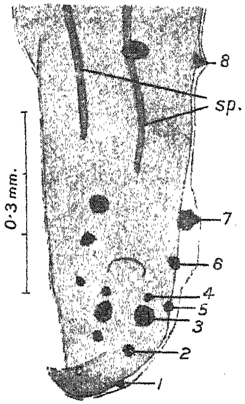
GNATHOSTOMIDÆ.



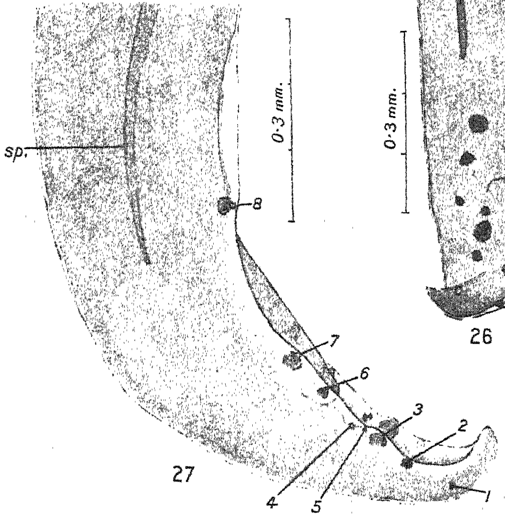
24



25



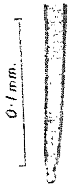
26



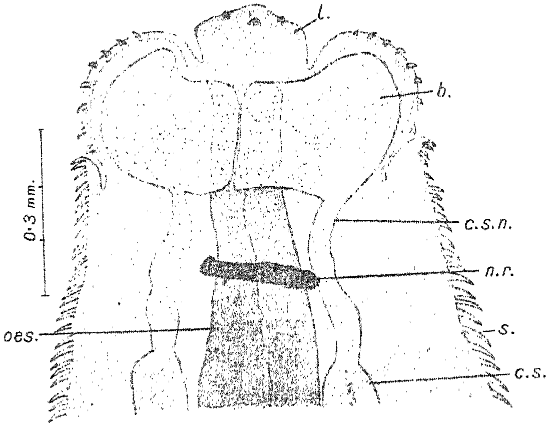
27

Bale & Danielsson, Ltd

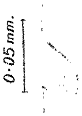
GNATHOSTOMIDÆ.



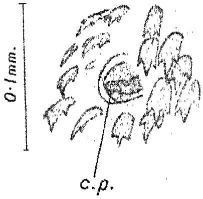
28



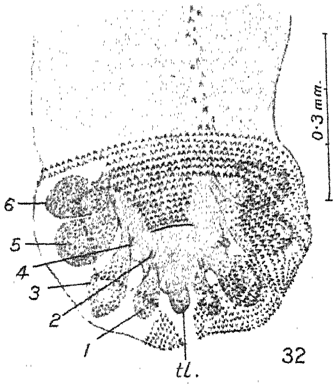
29



31



30

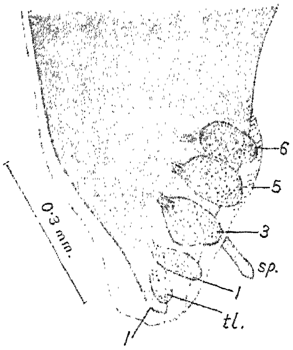


32

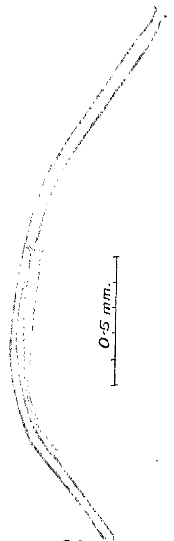
Bale & Danielsson, L^{td}.

GNATHOSTOMIDÆ.

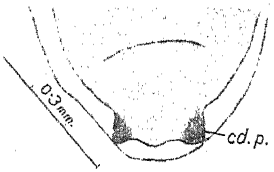
P. Z. S. 1920, BAYLIS & LANE, Pl. VIII.



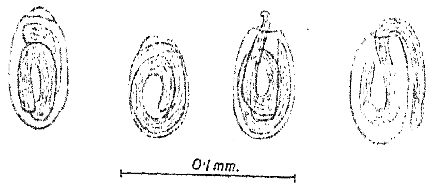
33



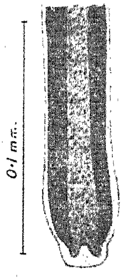
34



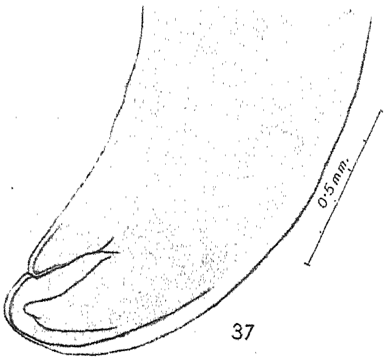
36



38



35



37

Bale & Danielsson, L^td

GNATHOSTOMIDÆ.

16. A Revision of the Nematode Family Gnathostomidæ.

By H. A. BAYLIS, M.A. Oxon., Assistant in the Department of Zoology, British Museum (Natural History), and CLAYTON LANE, M.D. Lond., Lt.-Col. I.M.S. (ret.)*.

[Received March 13, 1920: Read April 13, 1920.]

(Submitted for Publication by permission of the Trustees of the British Museum.)

(Text-figures 1–40; Plates I.–VIII.†)

Family GNATHOSTOMIDÆ ‡.

Cheiracanthidea Diesing (1861, p. 615).
Gnathostomidæ Railliet (1895, p. 1268).
Oxyuridæ (in part) Railliet and Henry (1916, p. 114).
Grathostomidæ Skrjabin (1916, p. 972) [misprint].
Heterakidæ (in part) Seurat (1918, p. 25).

This family of nematodes was founded by Railliet to include only the genus *Gnathostoma* Owen. Though the family-name appears constantly in text-books on medical and veterinary helminthology, a comparative study of the genera and species which appear naturally to fall into close relationship with *Gnathostoma spinigerum*, the type-species, has never, to our knowledge, been undertaken. Such relationships have, in some cases, been hinted at by previous writers. The genus *Tanqua* was tentatively referred to the family by Leiper (1908), while certain species of *Echinocephalus* have been referred by v. Linstow to *Cheiracanthus*, which is a synonym of *Gnathostoma*. One other genus, *Spiroxys* Schneider, 1866, the relationships of which have never been decided with any precision §, we now propose to include in this family, an inclusion which appears to necessitate a division of the family into two subfamilies. Certain other forms seem, from their existing descriptions, to be closely related (see p. 305), but in the absence of opportunities for re-examination of specimens we are obliged to be content with the mere suggestion of their affinities.

The chief family characteristic is the possession of a pair of large, fleshy, trilobed, lateral lips. Each lip is provided externally with three papillæ, while internally its cuticle is thickened and

---

* Communicated by the SECRETARY.

† For explanation of the Plates see p. 310.

‡ For family diagnosis, see p. 247.

§ Railliet and Henry (1916) place it among the Oxyuridæ, with *Labiduris* as its nearest ally. Seurat (1918) regards it as forming, with *Camallanus*, a subfamily, Camallaninæ, of the family Heterakidæ.

frequently raised into tooth-like prominences in the form of longitudinal ridges, which either meet or interlock with those of the other lip.

The œsophagus, in all the genera, is of a simple club-shaped type, increasing gradually in diameter from before backwards, muscular throughout, and without specially modified regions such as a bulb, gizzard, or glandular portion. In some species it is of considerable length, measuring up to about one-fifth of the total body-length. The usual valves are present at its opening into the intestine.

A pair of cervical papillæ, usually not prominent, is always present in both sexes, and the tail of the female is provided with a small pair of lateral papillæ.

The male possesses more or less well-developed caudal alæ, and two spicules are always present. The latter may be equal, subequal, or markedly unequal in length. In the majority of cases they have a characteristic ornamentation.

The species of all the genera are parasitic in the alimentary canal of their hosts, usually in its anterior part, and show a greater or less tendency to adopt a habit of burrowing in the tissues. Some of them are not infrequently found buried completely in the stomach-wall, where tumours tend to be formed round them at the expense of the host. Others, while not penetrating to this extent, obtain a very firm hold by burying their heads in the mucous membrane. One genus (*Gnathostoma*) has been found as a rare, and probably abnormal, parasite of man, its habitat in this case being the subcutaneous connective tissue and not the alimentary canal.

As indications of possible affinities outside the family, the following points are of interest:—

(1) In *Spiroxys* the caudal alæ of the male are developed into a "bursa" closely resembling that of *Physaloptera*, in that it is continued anteriorly across the ventral surface of the body.

(2) The genus *Hartertia* Seurat, 1915, appears, in some respects, to form a link between *Spiroxys* and such genera as *Physaloptera* and *Habronema*.

(3) In *Gnathostoma* the ventral surface of the caudal region, in the male, is partly covered with spinous processes, which may be compared with the low papilliform processes that cover this region in *Physaloptera*.

(4) The occurrence, throughout the family, of paired lateral lips suggests close affinity with the Spiruroidea or Spiruridæ (see footnote, p. 247).

It may be noted here that Stephens (in Fantham, Stephens, and Theobald, 1916) places *Gnathostoma*, *Tanqua*, and *Rictularia* in this family. Wedl (1862) also placed *Rictularia* near the Cheiracanthidea. Hall, however (1916), places it among the bursate nematodes.

Family Diagnosis.

GNATHOSTOMIDÆ Railliet, 1895.

Spiruroidea[*](?): with two large, trilobed, lateral lips, having the cuticle of their inner surfaces thickened and usually raised into longitudinal tooth-like ridges which meet or interlock with those of the other lip. Tail of male with more or less well-developed lateral alæ and two spicules. The vagina runs forward from the vulva before giving off the two or four uterine branches. Eggs with thin shells, ornamented externally with fine granulations.

Key to Subfamilies of Gnathostomidæ.

A. Cuticle behind the lips distended into a head-bulb by four submedian ballonets, a process from each of which extends into the body-cavity beside the œsophagus as a cervical sac	*Gnathostominæ* (p. 254).
B. Head-bulb, ballonets, and cervical sacs absent	*Spiroxyinæ*.

SPIROXYINÆ, subfam. n.[†]

These Gnathostomidæ are without head-bulb, cervical sacs, or ballonets. Their lips are characteristic. A deep cleft parts from the body the whole thickness of the dorsal and ventral edges of each, while the pulp of the middle lobe is separated from the pulps of the adjacent lobes by indentations so deep as to produce an appearance which has been aptly likened by Schneider (1866, p. 125) to the club on a playing-card (Pl. I. fig. 2, Pl. II. fig. 7). Each lobe carries a papilla, the subdorsal and subventral papillæ having conspicuous and the lateral papillæ inconspicuous terminations. The cuticle supporting the inner surface of each middle lobe is greatly thickened, and projects anteriorly beyond the edge of the lip as a sharp tooth-like prominence.

The cuticle of the tail in the male is expanded laterally into alæ and ventrally into vesicular swellings, which recall the ventral fusion of the alæ in *Physaloptera*. There are eleven pairs of caudal papillæ[‡], of which two pairs are definitely ventral, one pair lying in front of, the other behind, the cloacal opening; the other nine are more lateral. Of these lateral papillæ Nos. 2 and 5 are situated more ventrally than the others; six are postanal and three preanal, and in general the distension of the cuticle tends to cause their terminations to lie at the bottom of funnel-shaped depressions. Strong oblique ventral muscles occupy the whole distance between the cloacal opening and the anterior termination of the alæ, and may depress part of the preanal surface into the semblance of a sucker. There are two subequal, delicate, tapering spicules without flanges.

---

[*] Hall (1916) makes Railliet's superfamily Spiruroidea a synonym of Örley's family Spiruridæ, of the superfamily Filarioidea. If this system of classification is followed, there is no group of higher than family rank, embracing nematodes with paired lateral lips, to which the present family can be assigned. We therefore use the name of the superfamily Spiruroidea in this sense.

[†] For subfamily diagnosis, see p. 248.

[‡] NOTE.—Throughout our descriptions and in our figures we have numbered the caudal papillæ of the male worms consecutively from the extremity of the tail forwards—the first pair, or "No. 1," being that nearest to the tip.

In the female the tail, when seen from the side, has the dorsal surface convex and the ventral concave, and there is a notch on its ventral surface just anterior to the tip. The vulva lies near the middle of the body, whence the muscular vagina runs anteriorly before dividing into two thinner-walled uteri, the one running towards the head and the other towards the tail. The egg-shell is thin, colourless, oval, with fine external stippling, a clear space separating it from the granular contents.

The worms are found attached to, or buried in, the wall of the stomach of tortoises in Europe, Asia, and Africa, and possibly America.

The subfamily contains only the genus *Spiroxys*.

Subfamily Diagnosis.

SPIROXYINÆ.

Gnathostomidæ: without head-bulb, ballonets, or cervical sacs; lips wide, with a narrowed base and a trefoil-shaped pulp, and having the internal cuticle of the middle lobe much thickened, the point of the thickened portion projecting anteriorly as a sharp tooth; caudal cuticle of the male expanded into lateral alæ and a preanal vesicular swelling and bearing two pairs of ventral papillæ, one in front of and one behind the cloacal opening, and nine pairs of lateral papillæ of which six are postanal and three preanal, and which, by reason of the cuticular distensions, frequently appear to lie at the bottom of funnel-shaped depressions; spicules delicate, tapering and subequal; vulva near the middle of the body; the vagina running anteriorly; the two uteri opposed: ova with thin, colourless, stippled shell, from which the unsegmented granular contents are separated by a space.

Generic Diagnosis.

SPIROXYS* Schneider, 1866.

Spiroxys Schneider (1866, p. 125).
Spiroxis Schneider (1866, p. 29) [misprint].
Spiroptera (in part) Rudolphi (1819, pp. 25 & 242).
? *Ascaris* (in part) Rudolphi (1809, p. 193; 1819, pp. 25 & 242).
? *Physaloptera* (in part) Leidy (1856, p. 53).

The genus has the characters of the subfamily.

Genotype: *Spiroxys contorta* (Rud., 1819).

---

* For key to species, see p. 249. For measurements, see Table I., p. 253.

Key to Species of *Spiroxys.*

A. Lobes of the lips unarmed....................................	*S. contorta.*
B. Each of the three lobes of each lip carries close to either edge of its inner surface a sharp cuticular tooth.	*S. gangetica* (p. 251).

1. Spiroxys contorta * (Rud., 1819). (Text-figs. 1–3; Pl. I. figs. 1–4; Pl. II. fig. 5.)

Spiroptera contorta Rudolphi (1819, pp. 25 & 242).
Spiroxys contorta Schneider (1866, p. 125).
„ „ v. Linstow (1909, p. 58, figs. 22 *a*, 22 *b*).
Spiroxys contortus Railliet and Henry (1916, p. 114).
? *Spiroxys contortus* (Rud.) Seurat (1918, p. 23).
? *Ascaris testudinis* Rudolphi (1809, p. 193; 1819, pp. 25 & 242).
? *Physaloptera contorta* Leidy (1856, p. 53).

We have examined two sets of specimens of this nematode belonging to the collection of the British Museum (Natural History), one from Siebold's collection (which had been removed from the stomach of *Emys orbicularis* [*E. europæa*]) small, without eggs, and presumably immature; the other mature and labelled "from a water tortoise." They have no specific differences.

The worms are much twisted. Schneider describes the body as being always bent towards the ventral aspect. This appears to be at least usually the case, many of our specimens having an elbow-like bend in the neck-region. The head end (Pl. I. figs. 1 & 2) is very slender. Thence the diameter of the body gradually increases, nor does it again diminish till close to the anus. Except for characters common to the genus the lips are unarmed. In dorsal (or ventral) view (Pl. I. fig. 1) the tip of the dorsal (or ventral) lobe, particularly its pulp, is hooked posteriorly, while its anterior edge is rounded off.

In the male the caudal alæ (Pl. I. figs. 3, 4; Pl. II. fig. 5) are well-marked; the amount of their distension, and of that of the ventral cuticle between them, varies, but there appears to be regularly a considerable swelling of the latter just before the alæ cease anteriorly (Pl. II. fig. 5). The ventral papillæ are sessile (Pl. I. fig. 3). The spicules (Pl. I. figs. 3, 4; Pl. II. fig. 5) are long, slender, tapering, and transversely striated, have the appearance of being hollow, and end in a very fine point (text-fig. 1). They do not carry alæ, as was supposed by Schneider.

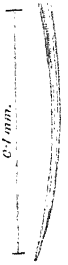
In the female the ventral caudal notch is relatively coarse (text-fig. 2). The female organs (text-fig. 3) have the generic characters.

In introducing the name *Spiroptera contorta*, Rudolphi (1819) mentions it as synonymous with *Ascaris testudinis.* He had previously (1809, p. 198) given as his authority for the latter name Braun (in Schneider, 1789), but expressly mentions that he has been unable to obtain the appendix in which this name appears. We also have failed. Since Stiles and Hassall (1905) do not mention this name in dealing with this genotype, we have presumed that it is a *nomen nudum* and have disregarded it.

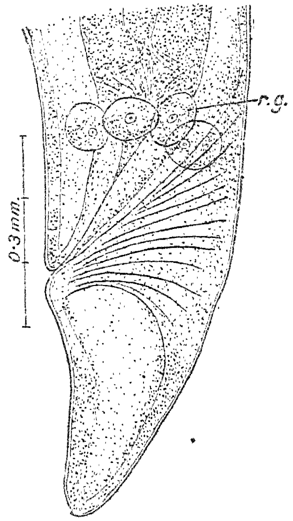
---

* For specific diagnosis, see p. 251.

Text-figure 1.*

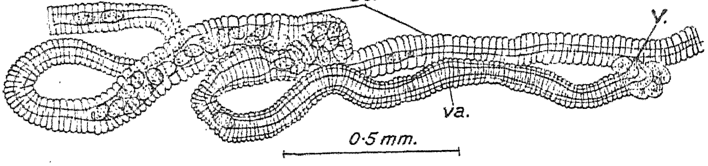


Text-figure 2.



Text-fig. 1.—*Spiroxys contorta.* Terminal portion of spicule.
Text-fig. 2.—*Spiroxys contorta.* Tail of female; lateral view.

Text-figure 3.



Spiroxys contorta. Female genital organs. (Mature specimen.)

It is necessary to mention Leidy's (1856, p. 53) *Physaloptera contorta* as a possible synonym. His description is as follows:—"Body capillary, most narrowed anteriorly with the posterior four-fifths spirally contorted; white, with the intestine brown. Lips prominent, constricted from the body, trilobate. Tail short, conical, acute, in the male with narrow alæ each furnished with five funnel-shaped pores.

---

* For explanation of lettering, see p. 310.

"Length of the female six lines to an inch; breadth to one quarter of a line; male from one-half to three-fourths of the size.

"Frequent in the stomach of *Emys serrata*, *Emys reticulata*, *Cistudo carolina*, and *Kinosternum pennsylvanicum*, adhering to the mucous membrane in the same manner as *Physaloptera constricta*" (*vide infra*, p. 272).

The general appearance, the shape of the lips, the "funnels" of the caudal papillæ in the male, and the habitat and hosts all suggest that this species is either identical with or closely allied to *Spiroxys contorta*, but since the type of Leidy's species cannot now be traced, the question must remain an open one.

With regard to the *Spiroxys contortus* (Rud.) of Seurat (1918), from the African tortoise, *Clemmys leprosa*, we find the description of this form somewhat difficult to understand. If our interpretation of it is correct, Seurat's worm differs from the European species in the following points:—

(1) the presence of an internal tooth on *each* lobe of each lip;
(2) the presence of a pair of large papillæ on the middle lobe of each lip, instead of one small papilla;
(3) the presence of an adanal, lateral pair of genital papillæ in the male;
(4) the presence of an accessory piece in the male.

Specific Diagnosis.

SPIROXYS CONTORTA (Rud., 1819).

A slender *Spiroxys*; the lips without special armature, the tips of the dorsal and ventral lobes, especially their pulp, hooked posteriorly; spicules ending in a very fine point; caudal notch of female relatively coarse.

2. SPIROXYS GANGETICA *, sp. n. (Text-figs. 4–6; Pl. II. figs. 6–10.)

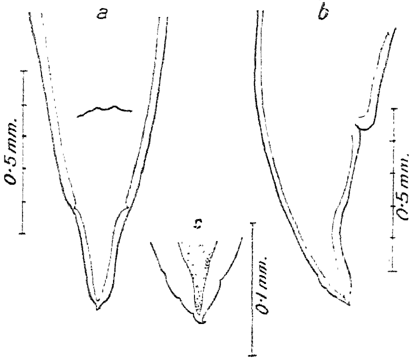
We have examined two batches of nematodes belonging to this species, the one collected by Mr. Southwell from a host indentified by him as *Trionyx gangeticus*, and the other collected by one of us (C. L.) from a tortoise killed in the Ganges delta, probably *Trionyx gangeticus*. The two sets of specimens are specifically identical.

This worm is stouter than the genotype. The head end tapers much more gradually than the tail and is usually bent at an angle. Close to either edge and near its base each lobe of either lip bears a cuticular tooth on its inner surface (Pl. II. figs. 6 & 7). Each lip, that is, has six teeth in addition to that characteristic of the genus. In dorsal (or ventral) view the inner face of the dorsal (or ventral) lobe is flattened against its fellow of the other lip, the cuticular teeth appearing from beneath near the angles so formed (Pl. II. fig 6). The male has well-developed caudal alæ (Pl. II. figs. 8 & 9), the lateral papillæ being correspondingly buried. The ventral papillæ are stalked and cup-shaped or forked at their ends. The lateral papillæ are more widely separated than those of the genotype. The spicules are ornamented with granulations tending to arrange themselves in transverse rows, and each has a blunt tip surmounted by a clear chitinous cap (Pl. II. fig. 10).

---

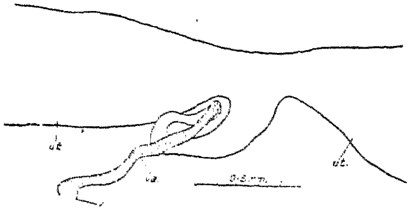
* For specific diagnosis, see p. 253.

Text-figure 4.

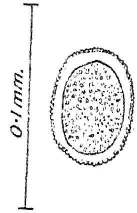


Spiroxys gangetica. Tail of female: *a*, ventral view; *b*, lateral view; *c*, lateral view of tip, at a higher magnification, to show the "notch."

Text-figure 5.



Text-figure 6.



Text-fig. 5.—*Spiroxys gangetica.* Female genital organs.
Text-fig. 6.—*Spiroxys gangetica.* Ovum.

In the female the tail is relatively more slender than in the genotype both in lateral and in ventral views, while the notch near its tip and the hook formed by it are particularly delicate (text-fig. 4, *c*). The generative organs (text-fig. 5) and eggs (text-fig. 6) are of the generic type.

Specific Diagnosis.

SPIROXYS GANGETICA.

A stoutish *Spiroxys*; each lip carries a special armature of six fine sharp teeth, one on either edge of each lobe; the flattened inner surfaces of the dorsal and ventral lobes are applied to those of the opposite side; spicules end in a blunt point; caudal notch in female very fine.

TABLE I.—Measurements of the Species of *Spiroxys*.

(All measurements in millimetres.)

	S. contorta.		*S. gangetica.*	
	♂.	♀.	♂.	♀.
Length	15–25	20·4–30	39–43	48–50·3
Thickness	0·5–0·7	0·45–0·6	0·75	0·85–0·95
Lips: dorso-ventral diameter....................	0·11-0·13	0·13	0·11-0·13	0·13
Lips: length	0·05–0·06	0·06–0·07	0·14–0·16	0·16–0·2
Distance between striations of body	0·005	0·004	0·0125	0·013–0·0175
Distance from head-end to cervical papillæ...	0·65–1·0	—	1·2-1·275	1·125–1·5
„ „ „ nerve-ring	0·4–0·6	0·5–0·7	0·75–0·825	0·8
„ „ „ end of œsophagus	1·9-3·6	2·4–3·0	3·9	4 to 4·3
„ „ „ excretory pore ...	0·45–0·75	0·6	0·925-1·15	0·9–1·0
Length of tail	0·3–0·4	0·5–0·55	0·35	0·65
Length of spicules	2·37–3·0	—	R. 2·1 L. 2·25	— —
Distance from tip of tail to vulva	—	8·2-13·6	—	20–27
„ „ „ caudal papillæ (♀)	—	Not seen.	—	0·32
Size of ova (maximum)	—	0·07×0·05	—	0·06×0·04

TABLE II.—Hosts and Distribution of the Species of *Spiroxys*.

Species.	Host.	Locality.	Recorder.
S. contorta.	*Emys* [*Testudo*] *orbicularis.*	Europe.	Rudolphi (1819).
	„ „ [*E. europea.*]	„	Schneider (1866).
	Emys [*Testudo*] *orbicularis.* [*E. lutaria.*]	„	v. Linstow (1909).
	Emys [*Testudo*] *orbicularis.* [*E. europea.*]	„	Baylis & Lane (present paper).
	Emys [*Testudo*] *orbicularis.* ("Water-Tortoise.")	„	„ „
	Emys serrata.	N. America.	Leidy (1856). [Recorded as *Physaloptera contorta.*]
	Emys reticulata.	„	„ „
	Cistudo carolina.	„	„ „
	Kinosternum pennsylvanicum.	„	„ „
S. gangetica.	*Trionyx gangeticus.*	India.	Baylis & Lane (present paper).

GNATHOSTOMINÆ *, subfam. n.

The members of this subfamily are characterized by the possession, immediately behind the lips, of a cuticular swelling, which we term the "head-bulb." This head-bulb always contains four subglobular, submedian, membranous structures, for which we use the expression "ballonets." Each of these is connected by a narrow neck with one of the four organs which have been called by several authors "cervical glands," but which we prefer to name "cervical sacs." The latter are elongated, apparently unicellular, thick-walled, hollow, blind organs hanging freely into the body-cavity at the sides of the œsophagus. Externally they are provided with a coat of fibrils showing a spiral arrangement (text-fig. 17) and probably contractile. The protoplasm lining the sac internally probably secretes a fluid into the lumen.

The cuticle of the head-bulb may be simply raised into transverse ridges or pronounced striations with projecting posterior edges: or the striations may be beset with rows of chitinoid hooks, strongly resembling the "rose-thorn" type of hooks found in certain Cestodes, such as *Dipylidium*. The hooks are embedded by means of their own roots in the cuticle, and are not merely outgrowths of the cuticle itself.

The external surface of the head-bulb may be unaffected by the presence of the ballonets within; or may be indented between the ballonets so as to give an external expression of the internal structure. Between the ballonets, sometimes pushing in the ballonet-membranes before them, certain muscles run up to the lips, crossing the cavity of the head-bulb obliquely in such a way that when contracted they serve to shorten the head-bulb in an antero-posterior direction. The function of the head-bulb is probably to act as a burrowing-organ or holdfast. The worms presumably first bury their heads in the tissues of the host while the head-bulb is in a deflated condition, and then the cervical sacs, contracting, force their contained fluid into the ballonets, thus distending the head-bulb. The cuticular striations and hooks are additional structures rendering the whole apparatus more effective.

These various structures, with the exception of the ballonets, have been noted by previous writers, but quite a different interpretation has usually been put upon them. Fedchenko (1872), working on *Gnathostoma hispidum*, seems, according to our translator, to have believed that the matter inside the head was secreted by the four cervical sacs, and he thus comes nearly to our own conclusion. He notes the structureless necks into which the sacs pass, but has observed no actual connection between the sacs and the head-bulb. On the other hand, the prevailing interpretation is due to v. Linstow, who describes

---

* For subfamily diagnosis, see p. 255.

(1893) in the same species an elaborate arrangement by which ducts from the two cervical sacs of each side unite into a common duct, each common duct piercing the corresponding lip and opening on its outer surface by a conspicuous pore 0·013 mm. in diameter. The same author (1904*a*) has also described a similar arrangement of ducts in *Tanqua tiara*.

von Rátz (1900), for *Gnathostoma hispidum*, and Leiper (1909), for *G. siamense*, follow the very circumstantial description of v. Linstow.

The ballonets, or rather their contents, seem to be referred to by v. Linstow as the "Marksubstanz" of the head-muscles, but their essential nature, as closed membranous sacs, has escaped the attention of all these observers. Now, in viewing the head of one of these worms as a transparent object, it is easy to mistake the muscles that run across the head-bulb for continuations of the cervical sacs, or ducts connecting them with the exterior. One of us (Baylis, 1916) fell into this error in the case of *Tanqua*, and suggested the presence of pores on the anterior surface of the "striated swellings" (*i.e.*, the head-bulb). This is the chief mistake into which other observers have probably fallen. The "pore" on the outer surface of the lip described by v. Linstow in *Gnathostoma* corresponds in position to the lateral papilla which we find throughout the subfamily. This papilla sometimes terminates in a little "dimple" of the cuticle, which might give it the appearance of a pore; furthermore, when seen in transverse section, as in v. Linstow's case, the large nerve running up to the papilla might easily give the impression of a duct. The central portion of the nerve then has a reticulate appearance, and under a low power rather suggests the lumen of a duct.

We have been able to trace the cervical sacs into the ballonets, but are unable to find any external opening, in series of sections of *Echinocephalus* and of *Tanqua* (text-fig. 10), and there seems to be no reasonable doubt that the arrangement is similar in all the genera and species.

Subfamily Diagnosis.

GNATHOSTOMINÆ.

Gnathostomidæ: with a cuticular head-bulb provided either with marked transverse striations or with rows of backwardly-directed hooks, and containing four membranous, submedian ballonets, the cavity of each of which is in communication with one of four elongated, blind, cervical sacs hanging freely in the body-cavity.

Habitat (adult): stomach or intestine (exceptionally other parts of the body) of fishes, reptiles, and mammals.

Type-genus: *Gnathostoma* Owen, 1836.

Key to Genera of Gnathostominæ.

A. Head-bulb furnished with transverse cuticular ridges having sharp, backwardly-projecting edges, but without hooks	*Tanqua.*
B. Head-bulb armed with transverse rows of recurved hooks.	
a. Body unarmed	*Echinocephalus* (p. 273).
b. Body partially or wholly armed with backwardly-directed spines	*Gnathostoma* (p. 291).

TANQUA * R. Blanchard, 1904.

Ascaris (in part) v. Linstow (1879, p. 320).
„ „ Stossich (1896, p. 52).
Heterakis (in part) v. Linstow (1904 *a*, p. 97).
Ctenocephalus † v. Linstow (1904 *a*, p. 102).
Tanqua R. Blanchard (1904, p. 478).
Tetradenos v. Linstow (1904 *b*, p. 301).
„ „ (1906, p. 173).

This genus is characterized by having the large cuticular head-bulb unarmed, but marked with coarse and very distinct transverse striations, having their posterior edges projecting so as to give the outline of the bulb a more or less serrated appearance in optical section.

A former brief account given by one of us (Baylis, 1916) of this genus requires some correction in the light of further work. Thus the lips are definitely lateral, and the statement formerly made to the contrary (following the erroneous orientation of von Linstow) is withdrawn.

The lips are curiously asymmetrical, each being twisted slightly towards the dorsal or ventral side, in such a way that the teeth of the middle lobes cross each other like the blades of a pair of scissors. The dorsal and ventral lobes of each lip do not, as was formerly supposed, bear each a single tooth, but each is bilobed on the inner surface so as to form two teeth. There are thus five teeth on each lip, and these interlock with those of the opposite lip, giving a very close bite, which enables the animal to obtain a firm grip of the tissues of the wall of its host's stomach.

The head-bulb is divided by longitudinal indentations into either two (a dorsal and a ventral) or four (submedian) portions. In the interior of the bulb are contained the four ballonets with delicate membranous walls, the cavities of which are in communication with those of the four cervical sacs. When the head-bulb is divided into four swellings, each swelling contains one of the ballonets; while in the forms which have only two swellings, two ballonets are contained in each.

---

* For generic diagnosis, see p. 258.

† Not *Ctenocephalus* Kol., 1857 (dipteron).

The cuticle immediately behind the head-bulb always shows an invagination forming more or less of a "collar" round the neck. In one species this invagination is so highly developed that the worm can withdraw its entire head into a prepuce-like sheath of cuticle. In species in which the collar is less highly developed, portions of the host's tissues are not infrequently found caught between it and the back of the head-bulb, so that the collar appears to function as an accessory apparatus for enabling the worm to secure itself.

The cuticle of the body is thick and tough, and is marked with fine transverse striations, but otherwise smooth. The cervical papillæ are usually situated at about one-fourth of the length of the œsophagus from the anterior end. The excretory pore is situated at about the same level, or a little in front of it, on the ventral side. The œsophagus is usually rather long, and the cervical sacs relatively short, extending beside it to not more than one-third of its length.

The tail of the male is curled towards the ventral side, and is provided with strong oblique muscles for this purpose. The caudal alæ are rather well-developed, extending from a little in front of the cloacal aperture to near the tip of the tail. There are always eight pairs of caudal papillæ, which vary very little in arrangement in the different species. The papillæ are of different sizes, the largest being always those of the third, fifth, and seventh pairs. The fourth and sixth pairs are always small, and more ventral in position than the others. The cloaca opens at about the level of the fifth pair, and consequently the fourth and sixth pairs form a small, ventral, circum-anal group very much like that seen in *Spiroxys*. All the large papillæ in *Tanqua* show an extremely characteristic structure, having a very large, swollen, basal portion and a finger-shaped termination.

The spicules are equally characteristic. They are tubular, cylindrical, and equal in length, and always present a rasp-like appearance, owing to a covering of minute irregular granulations. Only the extreme tip is smooth, and this is usually of smaller calibre than the shaft of the spicule, forming a little rounded or conical projection.

As regards the female organs, the vulva is situated in the posterior half of the body. The vagina runs forward for a longer or shorter distance before opening into the uterus. The latter may consist of two or four branches. When two branches are present, they are opposed—*i.e.*, one runs forward and the other backward. When four are present, three turn forward and one backward. Various swellings, functioning as receptacula seminis or as egg-reservoirs, occur in the course of the uterine tubes, but their position does not seem to be constant. In fact, the general shape of the uterus varies so greatly in different specimens of the same species that the expansions of the tubes appear to be of a temporary nature, and cannot be made use of for systematic purposes.

It is a curious fact that the number of uterine branches in this genus appears to be in direct correlation with the number of external divisions of the head-bulb. In the forms parasitic in snakes, where the head-bulb is composed of two portions only, the uterus has two branches; while in *T. tiara*, where there are, in the adult, four swellings on the head-bulb, there are also four uterine branches.

Nothing is known of the development or life-history of any of the species of *Tanqua*. The hosts, so far as is known, are all carnivorous reptiles, and belong to semi-aquatic genera; and it is not unnatural to suspect that there may be an intermediate host which lives in or near fresh water, and is eaten by the final host.

Generic Diagnosis.

TANQUA * R. Blanchard.

Gnathostominæ: head-bulb coarsely striated transversely, unarmed, divided externally into two or four swellings containing the ballonets. Body unarmed. Each lip with five teeth, interlocking with those of the other lip. Cuticle behind the head-bulb forms a more or less pronounced collar or invagination. Tail of male with well-developed alæ and eight pairs of papillæ, of which the largest are the third, fifth, and seventh. The fourth and sixth pairs small, ventral, and forming a circum-anal group. The larger papillæ have a large swelling before the finger-shaped termination. Spicules equal, tubular, rasp-like, with smooth tip. Vulva in posterior half of body; vagina running forward from the opening. Uterus consists of two opposed branches, or of three anterior branches and one posterior. Eggs oval, with thin shell ornamented with fine granulations. Embryos not fully-formed at the time of laying.

Habitat: stomach of semi-aquatic lizards (Varanidæ) and semi-aquatic snakes (*Tropidonotus*, etc.).

Genotype: *T. tiara* (v. Linst., 1879).

Key to Species of *Tanqua* †.

A. Head-bulb with four swellings. Uterus with four branches, three anterior and one posterior. Parasitic in semi-aquatic lizards (Varanidæ)	*T. tiara* (p. 259).
B. Head-bulb with two swellings. Uterus with two branches, opposed. Parasitic in semi-aquatic snakes.	
a. Head retractile	*T. diadema* (p. 268).
b. Head not retractile..	*T. anomala* (p. 264).

---

* For measurements, see Table III., p. 270.

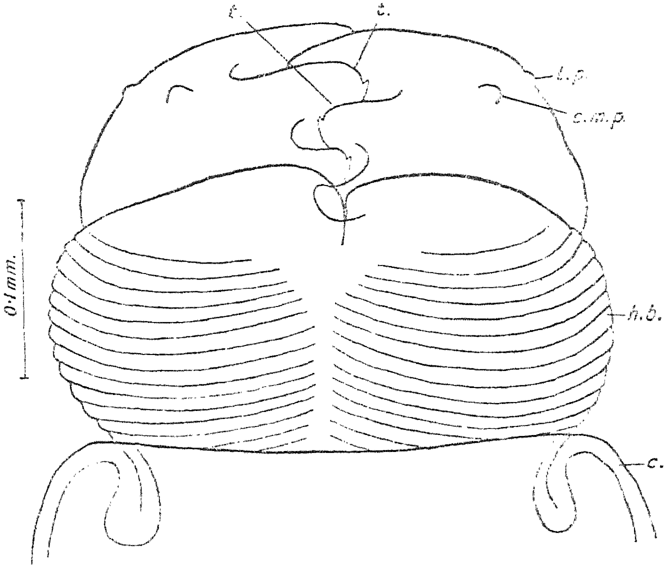
† For doubtful species, see p. 271.

1. TANQUA TIARA* (v. Linst., 1879). (Text-figs 7–15; Pl. III. figs. 11–13.)

Ascaris tiara v. Linstow (1879, p. 320: pl. v. fig. 1).
 ,, ,, Parona (1898, p. 114).
Ctenocephalus tiara v. Linstow (1904 *a*, p. 102; pl. ii. figs. 23–27).
Tanqua tiara R. Blanchard (1904, p. 478).
 ,, ,, Leiper (1908, p. 189).
 ,, ,, (in part) Baylis (1916, p. 224: text-fig. 1).
Tetradenos tiara v. Linstow (1904 *b*, p. 301).
 ,, ,, ,, (1906, p. 173).

The specimens from *Tropidonotus asperrimus*, previously referred by one of us (Baylis, 1916) to this species, have now been redetermined as *T. anomala* (v. Linst.) (*q. v.*), *T. tiara* being restricted to the forms from various species of Monitor lizards (Varanidæ). The description of the caudal papillæ of the male of *T. tiara* then given was correct, though the specimen figured (*l. c.*, text-fig. 2, p. 226) was not *T. tiara*, but *T. anomala*, which in this respect is hardly distinguishable from it. The structure of the female genital apparatus was not completely elucidated, and will be given here in greater detail.

Text-figure 7.

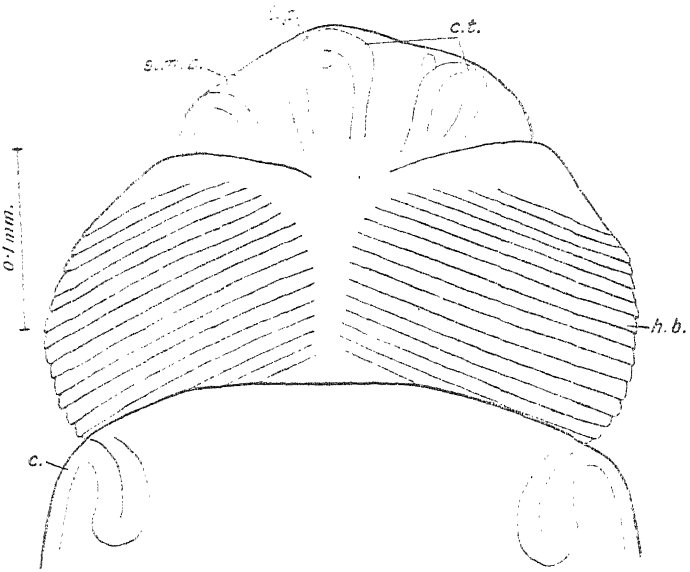


Tanqua tiara. The head; dorsal (or ventral) view.

---

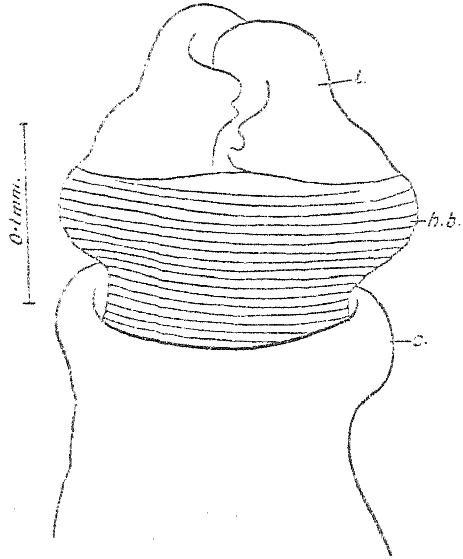
* For specific diagnosis, see p. 261.

Text-figure 8.



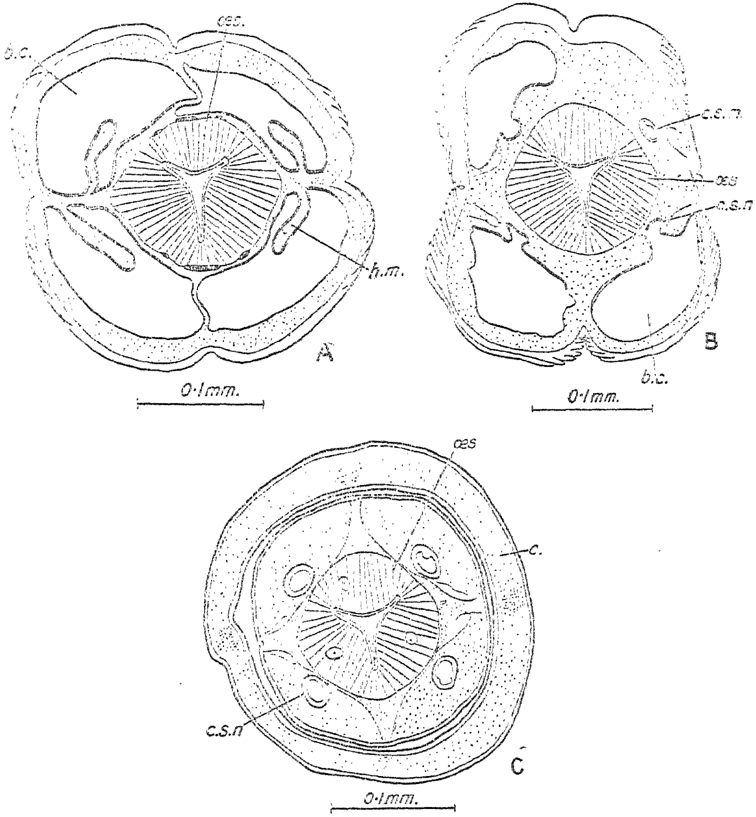
Tanqua tiara. The head; lateral view.

Text-figure 9.



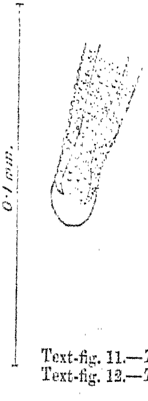
Tanqua tiara. Head of young specimen; dorsal (or ventral) view.

Text-figure 10.

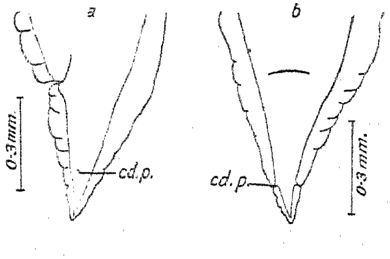


Tanqua tiara. Transverse sections through the anterior region. A, at about the middle of the head-bulb; B, at the back of the head-bulb; C, at the level of the cuticular collar.

Text-figure 11.



Text-figure 12.



Text-fig. 11.—*Tanqua tiara.* Terminal portion of spicule.
Text-fig. 12.—*Tanqua tiara.* Tail of female; *a*, lateral; *b*, ventral view.

The species appears to be widely distributed in India, Ceylon, the Malay Archipelago, Australasia, and Africa, and shows little local variation except in size.

The lips (text-figs. 7 & 8; Pl. III. fig. 11) are large and thick, and somewhat flattened in front as seen in a dorsal or ventral view (text-fig. 7). In very young specimens the shape of the lips is more conical (text-fig. 9). When the lips are viewed from the dorsal or ventral side (text-fig. 7), there is seen on the edge of each tooth a little pointed projection which appears to be the expression of a ridge running along the inner surface of the lip, and recalling the dentigerous ridges met with in certain Ascaridæ.

The head-bulb is large, and is distinctly divided (in mature specimens) into four swellings by longitudinal depressions in the mid-dorsal, mid-ventral, and mid-lateral lines (text-figs. 7 & 8; Pl. III. fig. 11). In very young examples (text-fig. 9), measuring from 5 to 7 mm. in length, and in which the lips are not yet fully formed, the head-bulb shows only two swellings, situated dorsally and ventrally. The transverse striations on the head-bulb (in the adult) are discontinued at the depressions which separate the four quarters of the bulb.

The collar-like cuticular invagination behind the head-bulb is well-marked. The œsophagus occupies about one-fifth of the total length. The cervical sacs are only about one-quarter of the length of the œsophagus, or less.

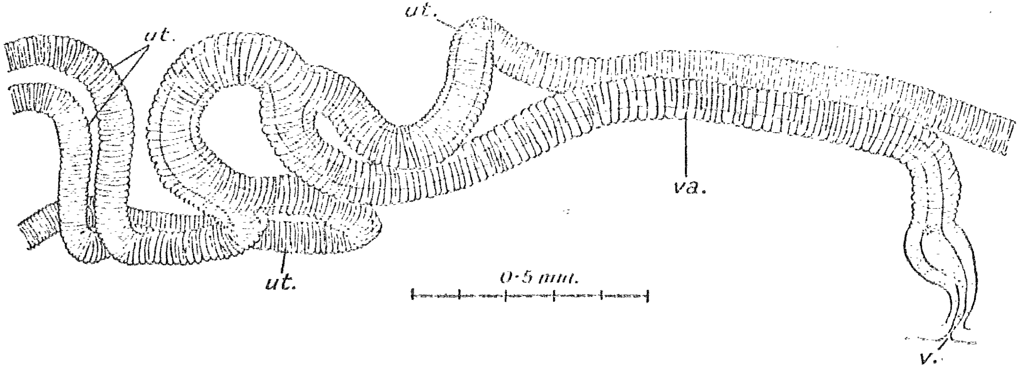
In the male the fifth, or adanal, pair of caudal papillæ (Pl. III. figs. 12 & 13) is the largest. The intervals between the second and third, and between the seventh and eighth, pairs are longer than the rest. The spicules have a small, smooth, rounded tip, just in front of which the diameter of the spicule is slightly reduced (text-fig. 11).

In the female the tail (text-fig. 12) is short, straight and conical. The female genital apparatus is highly characteristic. The vulva is situated towards the posterior end of the body, within the last quarter of the total length. The internal organs consist essentially of a vagina and four uterine tubes*, leading to four ovaries. The four divisions of the uterus are invariably arranged on the same general plan, three of them passing off towards the anterior and one towards the posterior end. A considerable amount of variation appears to exist, however, in their mode of origin. Sometimes (text-fig. 13) they appear to originate separately from a common narrow stem which is continuous with the vagina—first, the posterior branch comes off and sooner or later turns back more or less parallel with the vagina; then a little further forward one branch comes off and runs forward; and, finally, the common stem bifurcates at its

---

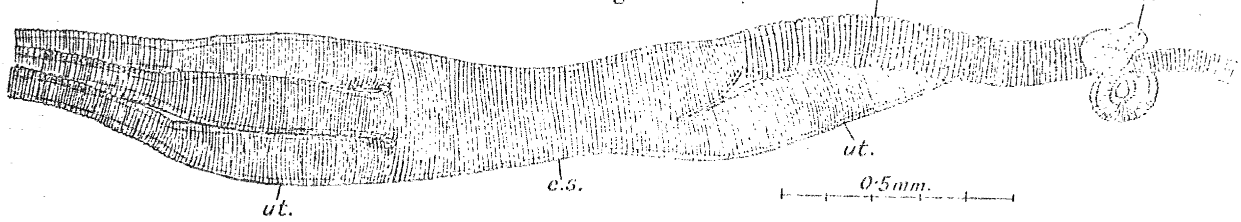
* In this connection it is interesting to note that another nematode from a Monitor (*Physaloptera varani* Parona, 1890 [=*P. quadrovaria* Leiper, 1908]) also has a four-fold division of the uterus.

Text-figure 13.



Tanqua tiara. Female genital organs. (Mature specimen from India.)

Text-figure 14.

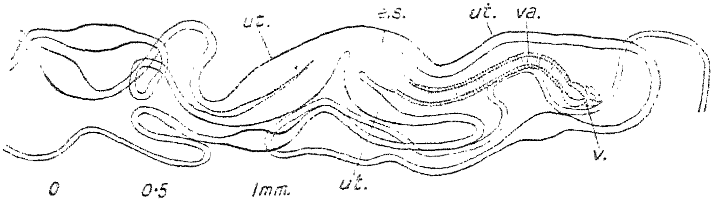


Tanqua tiara. Female genital organs. (Young specimen from Zanzibar.)

anterior end to form two parallel branches which also run forward.

At the opposite extreme we have observed cases (text-fig. 14) where the vagina runs into a more or less oblong, swollen uterine sac, which gives off a single branch at its posterior end and three branches side by side anteriorly. Between these extremes of variation there appear to be intermediate forms (text-fig. 15) in which the point of origin of the first of the three anterior branches shows a greater or less tendency to approach that of the other two. The shape of the common uterine chamber varies considerably. We are unable to recognize in these varieties in the form of the female organs any of systematic value, since we have found the same range of variation in material from both Indian and African sources, and since the extremes are, as has been stated, connected by intermediate forms.

Text-figure 15.



Tanqua tiara. Female genital organs. (Young specimen from Nigeria.)

Specific Diagnosis.

TANQUA TIARA (v. Linst.).

Head-bulb divided in the adult into four swellings, each containing a single ballonet. Head not retractile within the cuticular collar. Vulva within the last quarter of the body. Uterus with three anterior branches and one posterior.

Habitat: stomach of semi-aquatic lizards (Varanidæ).

For list of hosts, see p. 271.

2. TANQUA ANOMALA * (v. Linst., 1904). (Text-figs. 16–20; Pl. IV. fig. 14.)

Heterakis anomala v. Linstow (1904 *a*, p. 97; pl. i. figs. 10–11).

Tanqua anomala Baylis (1916, p. 229).

T. tiara (in part) Baylis (1916, p. 223; text-fig. 2).

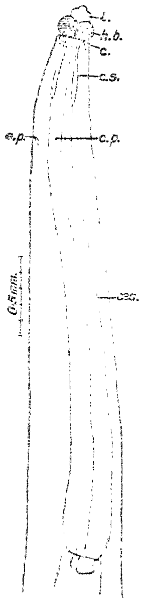
Of this species we have now, through the kindness of Dr. J. Pearson, of the Colombo Museum, had the opportunity of re-examining two of the original specimens. These were, unfortunately, both females, no male being available, but we have been able not only to confirm our suspicions as to the species belonging to the genus *Tanqua*, but also to compare the type-specimens with our own examples from Indian snakes, and to satisfy ourselves that these belong to the same species.

---

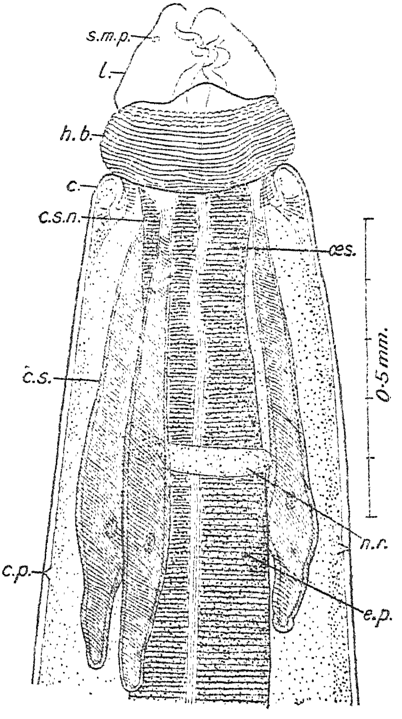
* For specific diagnosis, see p. 268.

This form appears to be very variable in size, while constant in other characters. The extreme size-variations we should certainly have been inclined to regard as being at least sub-species, had we been able to find any definite anatomical differences in support of this view. The type-specimens in the Colombo Museum, from *Tropidonotus piscator* in Ceylon, are among the smallest, while the largest examples we have seen came from a snake of another genus (*Homalopsis buccata*) in Siam.

Text-figure 16.



Text-figure 17.

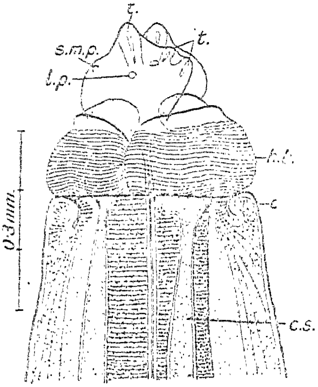


Text-fig. 16.—*Tanqua anomala*. Head and œsophageal region; lateral view. (The cervical sacs are unusually short in this specimen.)

Text-fig. 17.—*Tanqua anomala*. Anterior end; nearly ventral view.

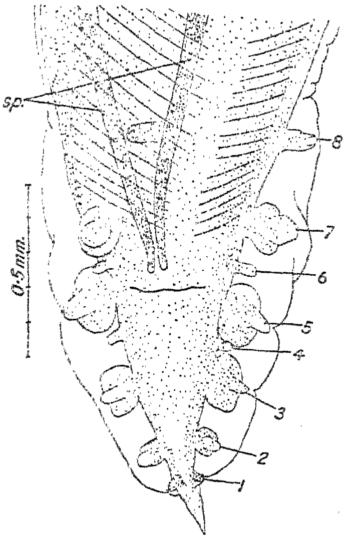
The anterior part of the body (text-fig. 16) is tapering. The lips (text-figs. 17, 18) are large and prominent, and more conical in shape, when viewed from the dorsal or ventral edge, than those of *T. tiara*. Some of the worms were received, in spirit, still firmly attached by the lips to the stomach-wall of the host, and it required a considerable pull to remove them.

Text-figure 18.



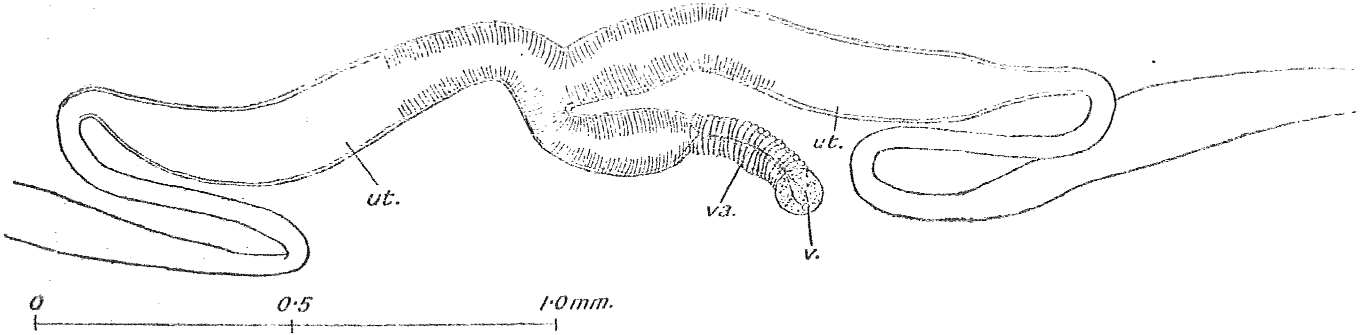
Tanqua anomala. Anterior end; lateral view.

Text-figure 19.



Tanqua anomala. Tail of male; ventral view.

Text-figure 20.



Tanqua anomala. Female genital organs. (Young specimen.)

The head-bulb (text-figs. 16–18) is, relatively to the size of the worm, very small. It consists of two hemispheres separated laterally but continuous dorsally and ventrally, and is thus comparable with that of very young examples of *T. tiara*. The striations are very well-marked.

The œsophagus occupies from one-twelfth to one-eighth of the total length. The cervical sacs (text-figs. 16 & 17) are relatively short, extending through, roughly, the first quarter of the length of the œsophagus.

There is nothing in the number, shape, or arrangement of the caudal papillæ of the male (text-fig. 19; Pl. IV. fig. 14) to distinguish this form from *T. tiara*. The preanal "sucker-like organ," referred to by v. Linstow (1904 *a*), appears to us to have been simply the terminal portion of the intestine, seen in optical transverse or oblique section by transparency through the body-wall. We can find no superficial sucker-like organ on the ventral surface.

The vulva is situated at about one-third of the body-length from the posterior end. The vagina is short, and opens at right angles into the uterus. The latter has two branches, which usually proceed at once from the termination of the vagina to run anteriorly and posteriorly respectively. In a young specimen from *Tropidonotus asperrimus* (text-fig. 20), the muscular vagina appeared to be very short, and continued as a common uterine tube for a short distance before the divergence of the two branches.

Specific Diagnosis.

TANQUA ANOMALA (v. Linst.).

Head-bulb divided in the adult into two swellings, situated dorsally and ventrally, each containing two ballonets. Head not retractile within the cuticular collar. Vulva at about the junction of the middle and last thirds of the body. Uterus with two opposed branches.

Habitat: stomach of semi-aquatic snakes (*Tropidonotus*, etc.).

For list of hosts, see p. 271.

3. TANQUA DIADEMA * Baylis, 1916. (Text-figs. 21–23; Pl. III. fig. 15; Pl. IV. fig. 16.)

Tanqua diadema Baylis (1916, p. 227; text-figs. 3, 4).

This species, which is now redescribed with some slight corrections, is readily distinguished from the preceding form from snakes by the prepuce-like fold of cuticle within which the head-bulb and lips can be completely retracted. The cuticle, especially anteriorly, is often very thick and wrinkled, reminding one of the condition frequent in *Gnathostoma*.

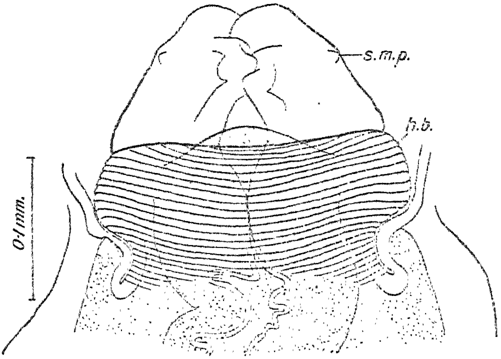
---

* For specific diagnosis, see p. 271.

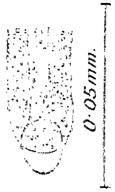
The head-bulb (text-fig. 21) is divided into two hemispheres, as in *T. anomala*. The lips (text-fig. 21) are rather large relatively to the head-bulb. The œsophagus occupies about one-tenth of the total length. The cervical sacs are short.

In the male the tail (Pl. III. fig. 15; Pl. IV. fig. 16) has rather wide alæ. The caudal papillæ are similar in number and arrangement to those of the other species. The second pair from the tip of the tail, however, are relatively small in some specimens, and do not always show the basal swelling to a very marked extent. The spicules are suddenly narrowed at the extremity to form a little, conical, smooth tip (text-fig. 22).

Text-figure 21.



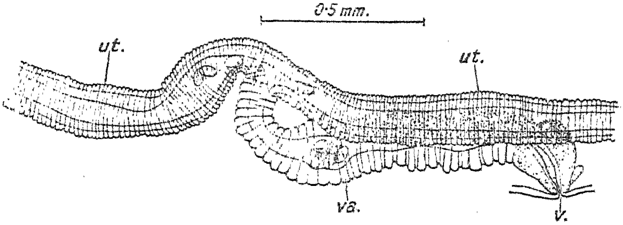
Text-figure 22.



Text-fig. 21.—*Tanqua diadema.* The head, with the cuticular sheath removed: dorsal (or ventral) view.

Text-fig. 22.—*Tanqua diadema.* Terminal portion of spicule.

Text-figure 23.



Tanqua diadema. Female genital organs. (Mature specimen.)

In the female the tail is tapering and sharply pointed. The vulva opens in the middle third of the body. The vagina (text-fig. 23) is short and thick. It opens at right angles into the uterus, the two branches of which at once pass off in opposite directions, without further subdivision.

TABLE III.—Measurements of the Species of *Tanqua*.

(All measurements in millimetres.)

Species	*T. tiara.*		*T. anomala.*		*T. diadema.*	
	♂.	♀.	♂.	♀.	♂.	♀.
Length	20–39	26–44	26·5–50	30·1–56	20–26	28–30
Thickness	0·55–1·1	0·9–1·4	0·8–2·0	0·95–2·0	0·6–0·95	0·8–1·0
Length of head	0·26–0·35	0·3–0·4	0·2–0·38	0·2–0·38	0·22	0·22
Transverse diameter of head-bulb	0·33–0·46	0·41–0·52	0·23–0·42	0·3–0·42	0·25	0·28
Distance from head-end to termination of cervical sacs	1·0–1·65	1·36–1·9	0·65–1·1	0·75–1·2	0·65	0·75
Dorso-ventral diameter of lips	0·22–0·3	0·22–0·35	0·14–0·24	0·18–0·2	0·15	0·18
Distance between striations of head-bulb	0·010–0·015	0·015–0·0167	0·009–0·016	0·0075–0·0125	0·0075	0·00625
Distance from head-end to cervical papillæ	0·9–1·33	0·975–1·35	0·75–0·95	1·03–1·15	0·5	—
„ „ „ nerve-ring	0·6–0·93	0·65–0·86	0·55–0·65	0·4–1·0	—	0·4
„ „ „ termination of œsophagus	4·5–9·5	5·0–9·0	3·0–5·1	3·6–5·3	2·2–3·0	3·0
„ „ „ excretory pore	0·84–1·2	1·0–1·2	0·725–0·95	1·0–1·075	0·54	0·5
Length of tail	0·5–0·7	0·3–0·65	0·45–0·9	0·4–1·3	0·6	0·65
Length of spicules	1·2–1·72	—	1·3–1·7	—	1·27	—
Distance of vulva from tip of tail	—	4·8–7·8	—	9·8–18·7	—	10·7
Distance between striations of body	0·004–0·005		0·0018–0·01		0·065	
Distance of caudal papillæ (♀) from tip of tail	0·1–0·175		0·25–0·38		0·25	
Size of ova (maximum)	0·075 × 0·045		0·065 × 0·05		0·06 × 0·0425	

Specific Diagnosis.

TANQUA DIADEMA Baylis.

Head-bulb divided in the adult into two swellings, situated dorsally and ventrally, each containing two ballonets. Head retractile within the cuticular collar, which forms a prepuce-like sheath. Vulva in middle third of the body. Uterus with two opposed branches.

Habitat: "intestines" (? stomach) of a snake, *Helicops angulatus*, in Brazil.

TABLE IV.—Hosts and Distribution of the Species of *Tanqua*.

Species.	Host.	Locality.	Recorder.
T. tiara	*Varanus "ornatus"* (probably *V. albigularis*).	Natal.	v. Linstow (1879).
	Varanus salvator.	Sumatra.	Parona (1898).
	„ „	Ceylon.	v. Linstow (1904 *a*).
	„ „	India.	Baylis & Lane (present paper).
[? *T. tiara*] ...	„ „ [*Hydrosaurus bivittatus.*]	Fed. Malay States.	Leiper (1908).
	Varanus gouldii.	Australia or New Guinea.	Parona (1898).
	Varanus bengalensis.	Ceylon.	v. Linstow (1904 *a*).
	Varanus niloticus.	White Nile.	Leiper (1908).
	„ „	Gold Coast.	Baylis (1916).
	„ „ [*V.* sp.]	Zanzibar.	„ „
	Varanus exanthematicus.	Northern Nigeria.	Baylis (1916) (specimens determined by Leiper).
T. anomala	*Tropidonotus piscator.*	Ceylon.	v. Linstow (1904 *a*).
	„ „	India.	Baylis & Lane (present paper).
	Tropidonotus asperrimus [= *T. quincunciatus*] (local form of *T. piscator*).	Ceylon.	Baylis (1916) [recorded as *T. tiara*].
	Homalopsis buccata.	Siam.	Baylis & Lane (present paper).
	"Water-snake."	India.	„ „
	"Snake."	„	„ „
T. diadema	*Helicops* [*Uranops*] *angulatus.*	Brazil.	Baylis (1916).

Doubtful Species of *Tanqua*.

ASCARIS SPHÆROCEPHALA Rud., 1809.

Rudolphi (1809, p. 188).

On account of certain resemblances between the characters of this species, as described by Rudolphi, and those of the worms of the Gnathostomid group, we mention it here for the sake of completeness. It is quite uncertain to what genus it belongs, but if Rudolphi's account of the head-bulb is correct it seems to approach more nearly to *Tanqua* than to any other. On the other hand, its host (a fish) and its habitat (the spiral valve of the intestine) suggest very strongly that it may have been an *Echinocephalus* (*q.v.*, p. 273). Rudolphi distinctly states, however, that the head-bulb is transversely *striated* and composed of two hemispheres, and he makes no mention of any armature of hooks or spines.

The species is briefly diagnosed as follows:—

"*Ascaris: membrana capitis utrinque semiorbiculari, striata; cauda obtusiuscula.*"

The following is a rough paraphrase of the further account (originally in Latin) of the worm, which was found in the lower part of the intestine of the Sturgeon, *Acipenser sturio*, in the spiral valve.

Worms an inch long, slender, white. Head spherical to naked eye, separated from the body by a constriction, and inflexed. Under the microscope a hemispherical membrane is seen on either side, transversely striated, giving the head a spherical shape. Mouth small, surrounded by three large, bluntly conical lips, joined at the apex, but not at the base, by lateral membranes, "so that they become obscured." Body smooth, attenuated at both ends, more so anteriorly. Tail rather blunt. Lips of vulva prominent, in third quarter of body. Alimentary canal like that of Ascarids. Eggs very peculiar, greatly elongated, blunt-ended (oblong-elliptical), clear at one end.

Rudolphi says (as we understand him) that on account of the general shape of the body and of the lips the worm belongs to the "Ascarides," but that the arrangement and "obscuring" of the lips [*sc.* by the "membrane" referred to] and the peculiar eggs mark it off as something different. His description suggests that the "three lips" he saw were the three tooth-bearing lobes of one lip, seen from the side by transparency, and the "membrane" joining them at the apex the cuticle of the outer or more lateral portion of the lip.

PHYSALOPTERA CONSTRICTA Leidy, 1856.

Leidy (1856, p. 53).

"Body white, with the brown intestine shining through, cylindrical to within a short distance of the extremities, incurved; anterior extremity with one or two constrictions, and abruptly inflexed. Lips large, lateral, constricted from the body, each trilobate. Tail of female incurved, abruptly conical and acute; of the male alated, with the alæ narrow, long, and turgid. Length of female $1\frac{3}{4}$ inches, breadth two-fifths of a line; male half the size.

"Found frequently in the stomach of *Tropidonotus sipedon*, with the anterior extremity of the body hooked through the mucous membrane, and very tightly adhering by means of the one or two constrictions."

The form thus described by Leidy so strongly suggests a *Tanqua*, both on account of several points in the brief description and on account of its host and habitat, that we feel obliged to include it in our account of the genus. It is impossible, however, without further investigation, to assign it to a definite position.

ECHINOCEPHALUS* Molin, 1858.

Echinocephalus Molin (1858, p. 154).
" " (1861, p. 311).
Cheiracanthus (in part) v. Linstow, in Shipley and Hornell (1904, p. 100).
" (in part) v. Linstow, in Shipley and Hornell (1905, p. 54).

Molin's original generic diagnosis was as follows:—

"*Caput discretum, echinatum; os orbiculare, terminale, magnum, inerme, vel armatum; corpus cylindricum, inerme, vel echinatum; vagina penis dipetala*; [*anus lateralis* †].—*Avium et piscium endoparasita.*"

Under this generic name two species were originally enumerated by Molin, *E. uncinatus* and *E. cygni*. The latter was regarded as a *species inquirenda*, leaving *E. uncinatus* the undisputed type-species. *E. cygni* belongs to the genus *Hystrichis*, and is, in fact, a synonym of *H. pachycephalus* Molin. Into the affinities of *Hystrichis* it is beyond our present scope to enter, but in spite of the rather strong superficial resemblance borne by some of its species to some of the Gnathostomidæ, we regard it as being of quite a different type from this group. Molin's generic characters for *Echinocephalus* seem, however, to have been based in part on the characters of *E. cygni*, and for this reason it becomes necessary to emend the diagnosis, besides adding to it from our own observations (see p. 275). Thus the "*os orbiculare*" and the statement that the genus is parasitic in birds as well as in fishes belong rather to *Hystrichis* than to *Echinocephalus*.

Molin (1861) rightly suggests the relationship of this genus to *Cheiracanthus* (*i. e.*, *Gnathostoma*). It shows equally great resemblances to *Tanqua*, and may, in fact, be looked upon as a *Tanqua*-like form complicated by the development of rows of spines or hooks along the cuticular ridges or "striations" of the head-bulb.

The lips are, in most cases, very similar in plan to those of *Tanqua*, and show a similar interlocking arrangement of the internal, tooth-like, cuticular ridges. In one form, however, the arrangement is complicated by the multiplication of the teeth on the dorsal and ventral lobes of the lips, so that each lip bears some 20 teeth altogether.

---

* For generic diagnosis, see p. 275.
† Added in 1861.

The head-bulb forms a continuous ring surrounding the base of the lips; it is never, in the species hitherto met with, divided externally into two or four swellings, as in *Tanqua*, though it still contains the same four ballonets connected with the cervical sacs. The latter sometimes end in a little button-like appendage (text-figs. 30, 33, *a*).

The size of the hooks on the head-bulb, the number of rows, and the number of hooks in each row, show considerable variety, and afford useful specific characters.

The body is smooth, as in *Tanqua*, the cuticle being, as a rule, finely striated transversely. The neck-papillæ are rather prominent. Molin's statement (1861) that the anus is lateral is entirely erroneous. The excretory pore is very inconspicuous, and is always to be found at about the same level as the cervical papillæ.

The tail of the male is coiled ventrally, and is provided with slight cuticular alæ, into which a series of paired caudal papillæ project. Of these there are always eight pairs, as in *Tanqua*, but the arrangement of the pairs differs somewhat in the different species. One constant feature is the long space separating the eighth or most anterior pair from the rest. Some of the papillæ are rather large, with a swelling at the base recalling that seen in *Tanqua*, but never so well-developed. The spicules are very characteristic. They are tubular and usually rather long and slender, the left spicule being apparently always a fraction of a millimetre longer than the right. Instead of the broken, external, rasp-like markings seen on the spicules of *Tanqua*, we find in *Echinocephalus* an irregular transverse striation, which only breaks up into a rasp-like pattern near the tip. The markings appear to be internal, the outer surface being smooth and transparent. The tip of the spicules consists of a thickening of the smooth outer layer only, and may be sharply pointed or somewhat blunt in different species.

The tail of the female is short and bluntly rounded at the tip. The vulva is invariably situated near the posterior end of the body, within a very short distance of the anus. The long vagina runs forward, and it seems to be characteristic of the genus that it forms a single coil in its course before opening into the uterus. The latter consists of a wide oblong egg-sac, which becomes very voluminous in the gravid female, and two horns which run forward from its anterior end. The ova have a finely granulated surface, and are of a similar oval shape to those of *Tanqua*. They do not contain fully-formed embryos when laid.

The adults are found in the intestine (usually in the spiral valve region) of sting-rays (Trygonidæ and Myliobatidæ). There is evidence that the development is indirect, requiring an intermediate host in the form of one of the bivalve molluscs upon which the final hosts feed. The larvæ of one species, at least, are found occupying cysts in the tissues of such bivalves as the pearl-oyster (see p. 277), where they appear to select chiefly the adductor muscle of the shell as their habitat.

Generic Diagnosis.

ECHINOCEPHALUS* Molin.

Gnathostominæ: head-bulb armed with transverse rows of hooks; not externally divided into swellings, but containing four ballonets internally. Body unarmed. No cuticular collar behind the head-bulb. Tail of male with slight alæ and eight pairs of papillæ, the most anterior pair always separated by a long interval from the rest. Spicules slightly unequal (left longer than right), tubular, long and slender, marked with transverse striations. Vulva near posterior end of body. Vagina long, opening into a wide uterine sac, which gives off two branches anteriorly. Eggs oval, with thin shells ornamented with fine granulations. Embryos not fully-formed at the time of laying.

Habitat (adult): intestine (usually in spiral valve region) of sting-rays and other Elasmobranch fishes.

Genotype: *E. uncinatus* Molin, *emend.* Baylis and Lane.

Key to Species of *Echinocephalus* (excluding *E. striatus* Mont.).

A. Head-bulb with not more than six rows of hooks......	*E. uncinatus.*
B. Head-bulb with more than six rows of hooks.	
a. Dorsal and ventral lobes of lips each with two teeth.	
a′. Head-bulb with 15 to 18 rows of about 150 to 200 hooks each	*E. southwelli* (p. 283).
b′. Head-bulb with 30 to 40 rows of very numerous hooks	*E. spinosissimus* (p. 277).
b. Dorsal and ventral lobes of lips each with a number (eight or more) of teeth.....................	*E. multidentatus* (p. 285).

1. ECHINOCEPHALUS UNCINATUS† Molin, 1858. (Text-fig. 24.)

Echinocephalus uncinatus (in part) Molin (1858, p. 154).

" " (in part) Molin (1861, p. 311; pl. xiii. figs. 7, 8).

Cheiracanthus uncinatus v. Linstow, in Shipley and Hornell (1904, p. 100; pl. iii. figs. 41, 44, 45–48).

Echinocephalus gracilis Stossich, in Shipley and Hornell (1906, p. 89).

The original description of this, the type-species of the genus, appears to us to have been based on two distinct species, both of which we have been able to recognize among our material. The head-bulb is described by Molin as having about 30 rows of small hooks in the male, and only six rows of larger hooks in the female. These two forms are also clearly figured in his later paper (1861). The size, number, and arrangement of the hooks, in our material, appear to give good and constant specific characters, and we feel little hesitation in concluding that Molin's male "*uncinatus*" corresponds to what will be described below as *E. spinosissimus* v. Linstow, while his female is a distinct form. We are, therefore, faced with the necessity of deciding which of Molin's two forms is to be designated as the type of *E. uncinatus*. A good and appropriate specific name already existing for the form with 30 or more rows of hooks, we have thought it advisable to retain it; and we feel justified in selecting Molin's female form, with 6 rows of hooks, as the true *E. uncinatus* *.

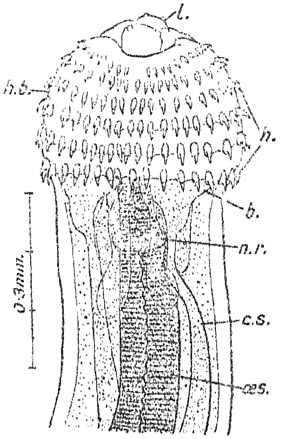
---

* For measurements, see Table V., p. 288.

† For specific diagnosis, see p. 277.

Our own material is scanty, consisting of one larval individual found encysted in a *Pinna* and three very young specimens from a sting-ray, *Myliobatis nieuhofi*. As none of these individuals contain fully-developed sexual organs, our description must remain incomplete.

Text-figure 24.



Echinocephalus uncinatus. Anterior end of larval specimen; lateral view.

The lips are not yet fully developed in any of the specimens, and we are unable to describe their structure. The head-bulb (text-fig. 24) is armed with 6 rows of hooks, each row containing between 40 and 50. The spines increase in size from before backwards. The neck-papillæ were not seen. Caudal papillæ could not be detected, nor was the position of the vulva yet visible. The cuticular striation is extremely fine and indistinct.

---

* The question of nomenclature is somewhat further complicated by the fact that Shipley and Hornell appear to have submitted larval forms of a species of *Echinocephalus* to both von Linstow and Stossich, and these two authorities held different opinions as to their identity. von Linstow ascribed them to Molin's species *uncinatus*, while Stossich created for them a new species, *gracilis*. We cannot, however, find anything in Stossich's (in Shipley and Hornell, 1906) remarks upon the larvæ to justify this step, and as the specimens are definitely stated by both authorities to have 6 rows of hooks, we regard the name *gracilis* as a synonym of *uncinatus*.

As regards the occurrence and life-history of this species, it seems fairly clear that it requires an intermediate host, in the shape of a bivalve mollusc, for its transference into the alimentary canal of its final host. Molin's original adult material was found in *Trygon brucco* in the Adriatic. von Linstow (in Shipley and Hornell, 1904) states that it also occurs in *T. pastinaca*. The larval stages are found encysted in the tissues of bivalves, usually in the adductor muscle of the shell. Thus they have been found fairly frequently in the pearl-oyster (see Shipley and Hornell, 1904, pp. 101–102), and we have now recorded their occurrence in *Pinna* sp. In the pearl-oyster the larvae are occasionally found "entombed in the nacreous lining of the shell" (Shipley and Hornell, 1904), where their shape is said to be wonderfully preserved.

In addition to the bivalves, the trigger-fishes, *Balistes mitis* and *B. stellatus*, are recorded by Shipley and Hornell (1904) as hosts for the later larval stages. It is not quite clear whether these fishes are regarded as a necessary second host of the parasite or not. The species of *Trygon* are said to devour both the *Balistes* and the oysters, but the presence of the worms in *Balistes* may have been abnormal. In these fishes they were found not only in the alimentary canal, but also in the peritoneum and connective tissue, in which they were thought to burrow by the help of the head-bulb, which was seen in both inflated and deflated conditions.

Specific Diagnosis.

ECHINOCEPHALUS UNCINATUS Molin, *emend.* Baylis and Lane.

Head-bulb with six rows of hooks, each row containing from 40 to 50 hooks.

For list of hosts, see p. 289.

2. ECHINOCEPHALUS SPINOSISSIMUS* (v. Linst., 1905). (Text-figs. 25–29; Pl. IV. figs. 17, 18.)

Echinocephalus uncinatus (in part) Molin (1858, p. 154).
" " " " (1861, p. 311, pl. xiii. figs. 5, 6).
Cheiracanthus spinosissimus v. Linstow, in Shipley and Hornell, (1905, p. 54, pl., figs. 12, 13).

This specific name was proposed by von Linstow for a form having 30 to 33 rows of hooks on the head-bulb, each row containing some hundreds of hooks. The host of the type-specimens was *Myliobatis aquila*, from the Gulf of Manaar.

---

* For specific diagnosis, see p. 283.

We believe, as has been stated above, that the male form described by Molin under the name of *Echinocephalus uncinatus* is referable to this species. The host, in this case, was *Trygon brucco*. Among our own material there are specimens from the sting-rays, *Trygon walga* and *Urogymnus asperrimus*, which appear to belong to the same species.

From their size (13·7 mm. in length) von Linstow's examples seem to have been immature, and few details are given of their internal stucture. We will therefore give a fuller description based upon our own material, chiefly upon the specimens from *Urogymnus*.

The worms are rather long and slender in general appearance. The largest female in our possession is not quite mature.

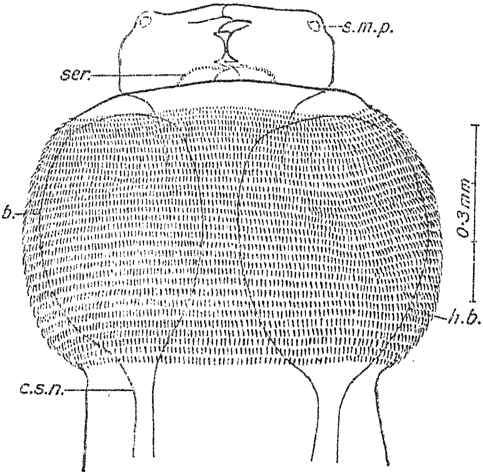
The lips (text-figs. 25 & 26) are large, very prominent and massive, each consisting of an outer portion bearing the three papillæ, and internally a rounded middle, and a dorsal and a ventral triangular, tooth-bearing lobe. These lobes meet those of the other lip and guard the mouth. The middle lobe is without teeth, while the other lobes are each provided with an internal thickening of the cuticle which is produced into tooth-like ridges (text-fig. 28). The teeth interlock, as in *Tanqua*, with those of the opposite lip. The posterior surface of the dorsal and ventral lobes bears a row of small tooth-like serrations (text-figs. 25, 26, *ser.*).

The head-bulb (text-figs. 25, 26) is distinctly marked off from the neck, and is visible to the naked eye as a little knob. The hooks (text-fig. 27) are very minute and very numerous. They are arranged in from 30 to 40 transverse rows, each row containing a very large number (several hundreds) of hooks. The rows are not always complete circles, but sometimes break off suddenly, while dichotomous branching of the rows is not infrequent.

The cuticular striation on the body is very fine. von Linstow's statement that the œsophagus is only $\frac{1}{45}$ of the body-length appears unintelligible, unless it is a misprint for $\frac{1}{4}$–$\frac{1}{5}$, and even in this case it does not agree very well with our own measurements.

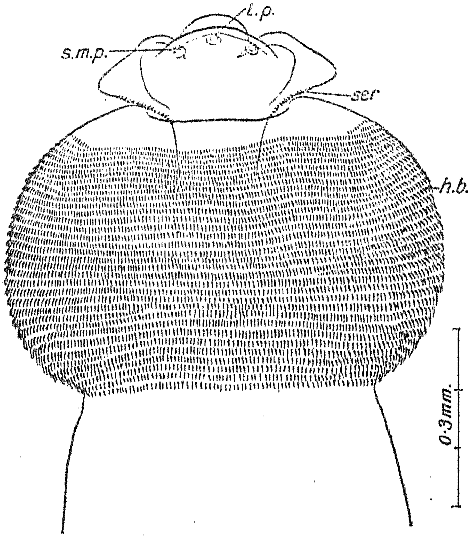
Of the eight pairs of caudal papillæ in the male (Pl. IV. fig. 17), those of the first pair are small and lateral, the second pair more ventral. Pairs 3 to 6 form a group on either side of the anus, the 6th pair being apparently adanal. The 5th pair is situated somewhat more laterally than the rest. These four pairs are placed close together, but a longer space separates pairs 2 and 3 and pairs 6 and 7. The 8th pair is separated by a very long interval from the 7th, and stands quite far forward, these last two pairs being both preanal. All the papillæ, except the small first pair, have a somewhat swollen base, not unlike the structure seen in *Tanqua*, though less strongly developed. The stout spicules (Pl. IV. fig. 17) are very slightly unequal in length, the left being the longer. Each spicule terminates in a smooth, conical point (Pl. IV. fig. 18).

Text-figure 25.



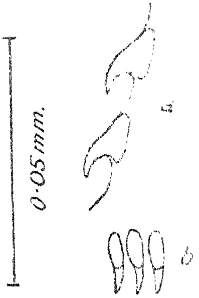
Echinocephalus spinosissimus. The head; dorsal (or ventral) view.

Text-figure 26.



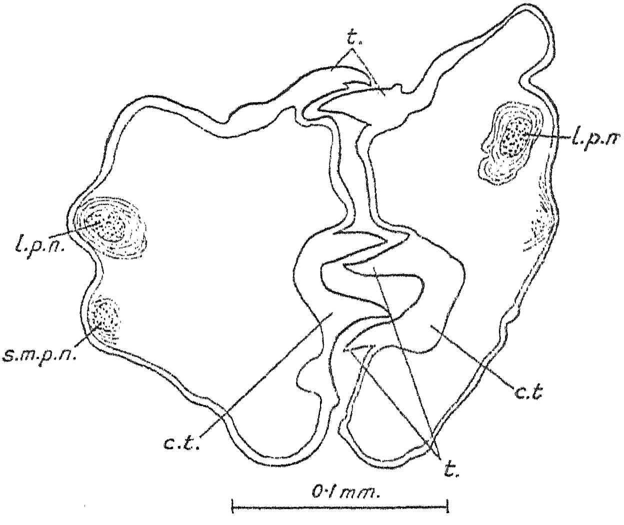
Echinocephalus spinosissimus. The head; lateral view.

Text-figure 27.



Echinocephalus spinosissimus. Hooks: *a*, in profile; *b*, in surface view.

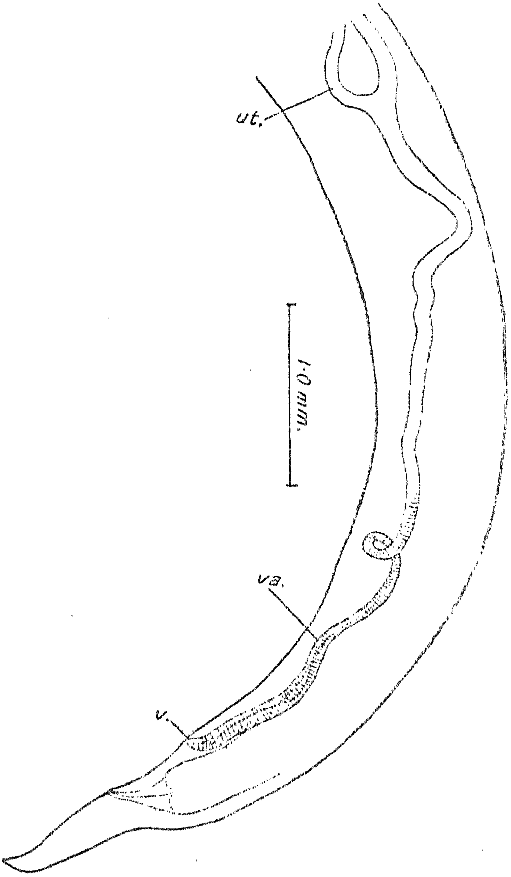
Text-figure 28.



Echinocephalus spinosissimus. Transverse section through the lips. (The section is somewhat oblique, passing through the middle lobe and only one outer lobe of each lip.)

The vagina (text-fig. 29) including the unpaired portion of the uterus, runs forward for nearly 5 mm. before giving off the two

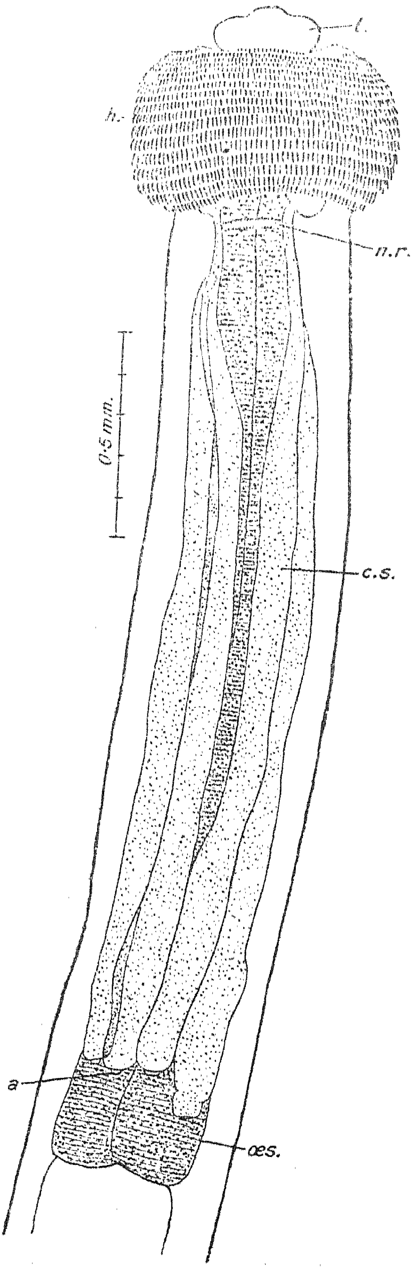
Text-figure 29.



Echinocephalus spinosissimus.
Posterior end of female; lateral view, showing genital organs.

uterine branches. We are unfortunately unable to describe the ova, none having been seen in a fully-developed condition in our specimens.

Text-figure 30.



Echinocephalus southwelli. Head and œsophageal region ; lateral view

Specific Diagnosis.

ECHINOCEPHALUS SPINOSISSIMUS (v. Linst.).

Head-bulb with 30 to 40 rows of hooks, each row containing several hundreds. Dorsal and ventral lobes of lips bear two teeth each.

For list of hosts, see p. 289.

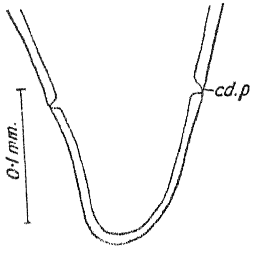
3. ECHINOCEPHALUS SOUTHWELLI*, sp. n. (Text-figs. 30–32; Pl. IV. fig. 19; Pl. V. figs. 20–23.)

This species, which we name in honour of Mr. Southwell, to whose kindness we are indebted for this and much of our other material, was also found in *Urogymnus asperrimus*. It is a form intermediate in several features between *E. spinosissimus* and a third species (*E. multidentatus*) to be described below, and all these three species were found together in the same individual host.

The present species is rather shorter and considerably more slender than *E. spinosissimus*.

The lips (Pl. IV. fig. 19; Pl. V. fig. 20) are rather squat, and their dorsal and ventral lobes bear only two teeth each, as in *E. spinosissimus*. The head-bulb (text-fig. 30), however, is much more like that of the next species, *E. multidentatus*, though smaller and less flattened antero-posteriorly. There are from 15 to 18 rows of hooks, which have a maximum length of 0·035 mm., and are thus intermediate in size between those of *E. spinosissimus* and *E. multidentatus*. The number of hooks in each row is also intermediate, there being, as nearly as can be estimated, from 150 to 200.

Text-figure 31.



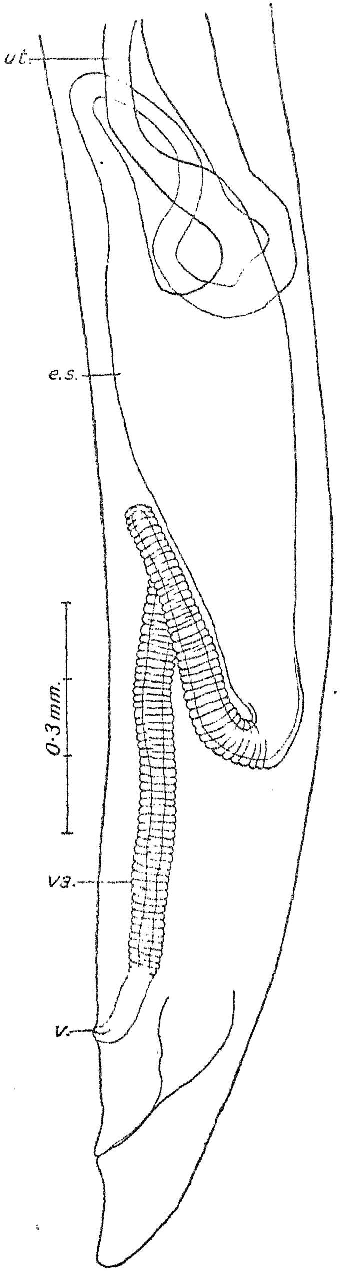
Echinocephalus southwelli. Caudal extremity of female; ventral view.

The cuticular striation on the body is rather coarse. The cervical sacs are nearly as long as the œsophagus. In the male, the first pair of caudal papillæ (Pl. V. figs. 21, 22), near the tip of the tail,

---

* For specific diagnosis, see p. 285.

Text-figure 32.



Echinocephalus southwelli. Posterior end of female; lateral view, showing genital organs.

are quite lateral; the 2nd, 5th, 6th, 7th, and 8th form a longitudinal series, while the 3rd and 4th are a little nearer to the mid-ventral line. Pairs 2–5 form a group rather close together, of which 2 and 4 are small papillæ and 3 and 5 relatively large. The intervals between 5 and 6 and between 6 and 7 are about equal, and greater than those between the posterior pairs, while a much longer interval separates 7 and 8.

The spicules (Pl. V. figs. 22, 23) are rather slender. A little before the tip each spicule is narrowed and then expanded somewhat, before terminating in a conical point.

In the female the tail (text-fig. 31) is very short. The vagina (text-fig. 32) leads into a very wide uterine sac.

Specific Diagnosis.

ECHINOCEPHALUS SOUTHWELLI Baylis and Lane.

Head-bulb with 15 to 18 rows of hooks, each row containing about 150 to 200. Dorsal and ventral lobes of lips bear two teeth each.

For list of hosts, see p. 289.

4. ECHINOCEPHALUS MULTIDENTATUS*, sp. n. (Text-figs. 33–36; Pl. VI. figs. 24–27; Pl. VII. fig. 28.)

This is the third species obtained from the sting-ray, *Urogymnus asperrimus*. In general naked-eye appearance it closely resembles *E. southwelli*, but is rather shorter and proportionately stouter. The head-bulb (text-fig. 33) is very conspicuous, and gives the worm much the appearance of a small nail.

The lips (Pl. VI. figs. 24, 25) are well-developed, but not prominent. In structure they are more complex than in any of the other forms studied by us. The outer portion bears the usual three papillæ, and the inner portion is, as usual, trilobed. The cuticle of the opposed inner surfaces of the dorsal and ventral lobes is raised into a number (from 8 to 11 on one lobe) of tooth-like ridges. These teeth are not constant in number or arrangement, and are not always symmetrical on the two lobes of the same lip, as may be seen in Pl. VI. fig. 25. Whether the teeth of the two lips can be interlocked is uncertain, though their appearance suggests that this is probably the case.

The head-bulb (text-fig. 33) is very wide compared with the neck which follows it, and is somewhat flattened antero-posteriorly. There are from 11 to 13 rows of large hooks (text-fig. 34). Each row may be estimated to contain some 100.

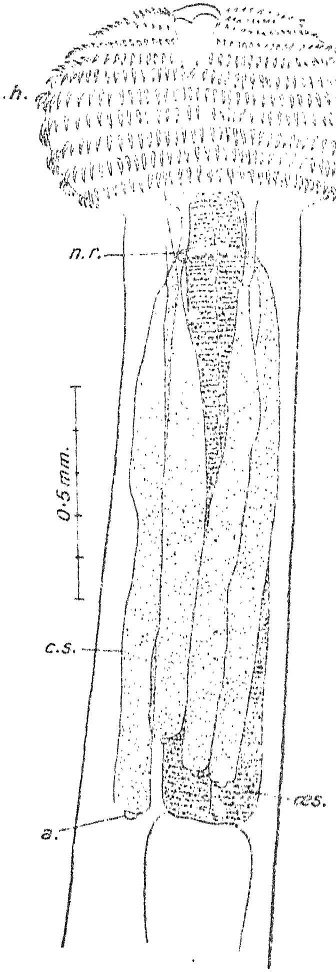
The cervical sacs are, as in *E. southwelli*, of approximately the same length as the œsophagus, both terminating at a point a little more or less than 2 mm. from the anterior extremity.

---

* For specific diagnosis, see p. 289.

The œsophagus is thus very short as compared with that of *E. uncinatus* and *E. spinosissimus*. The neck papillæ are prominent.

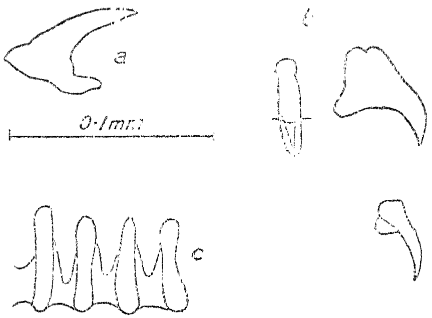
Text-figure 33.



Echinocephalus multidentatus. Head and œsophageal region; lateral view. (The triangular opening in the head-bulb is due to an artificial splitting of the cuticle.)

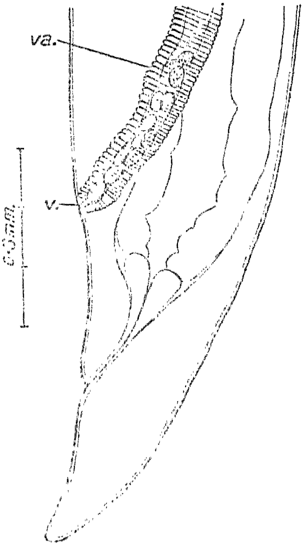
Of the eight pairs of caudal papillæ in the male (Pl. VI. figs. 26, 27), the first, as usual, is lateral, while the rest are more ventral in position. Pairs 1 to 5 appear to be postanal, 6 to 8

Text-figure 34.



Echinocephalus multidentatus. Hooks: *a* & *b*, various profile and surface views; *c*, a strip of cuticle with hooks, from a macerated specimen.

Text-figure 35.



Echinocephalus multidentatus. Posterior end of female; lateral view.

preanal. Pairs 3, 7 and 8 are conspicuously larger than the remainder. There is a long space between 7 and 8. Nos. 4 and 5 are small papillæ, one pair, which we call 4, being in a line with Nos. 2 and 3, while No. 5 is displaced laterally and posteriorly so as to lie at the same transverse level as No. 4. The papillæ project into a very feebly developed ala on either side. The

TABLE V.—Measurements of the Species of *Echinocephalus* (excluding *E. striatus* Mont.).

(All measurements in millimetres.)

Species ………… {	*E. uncinatus* (*larval forms only*).		*E. spinosissimus.*		*E. southwelli.*		*E. multidentatus.*	
	(a) From *Myliobatis.*	(b) From *Pinna*	♂.	♀.	♂.	♀.	♂.	♀.
Length	11·0	11·75	23·0–35·4	31·0	21·0	21·5	14·7–15·3	16·15–16·55
Thickness	0·4	0·45	0·55–0·8	0·86	0·5	[illegible]	0·55	0·6
Length of head	0·35	0·32	0·5–0·7	0·75	0·4–0·5	0·4–0·5	[illegible]	[illegible]
„ head-bulb	0·3	0·27	0·35–0·58	0·45	—	0·57	0·47	[illegible]
Transverse diameter of head-bulb	0·4	0·39	0·48–0·81	0·72	0·55	[illegible]	0·86	[illegible]
Distance from head-end to termination of cervical sacs	2·0	2·5	1·9–3·5	3·3–3·8	2·25	2·11–2·55	1·9–2·3	1·9–2·35
Dorso-ventral diameter of lips	—	—	0·21–0·41	0·41	0·22	0·21	0·3	[illegible]
Length of hooks on head-bulb	0·035	0·0175	0·0125–0·015	0·0125	0·035	0·035	[illegible]	[illegible]
Distance apart of rows of hooks	0·06	0·015–0·05	0·015–0·02	0·015	0·025	0·025	[illegible]	[illegible]
Distance from head-end to cervical papillæ	—	—	0·76–1·0	1·15	0·62	0·65	0·78	[illegible]
„ „ „ nerve-ring	0·4	0·45	0·6–0·7	0·8	0·47–0·55	0·42	0·65	0·65
„ „ „ termination of œsophagus	3·5	3·25	3·7–5·1	1·6–1·9	2·1	[illegible]	1·9–2·3	2·2–2·5
„ „ „ excretory pore	0·62	—	0·82–1·1	1·15	0·75	0·7	0·75	[illegible]
Length of tail	0·3	0·34	0·18–0·6	0·7–0·75	0·3	0·23	0·3	[illegible]
Length of spicules	—		R. 1·52–1·875	L. 1·55–1·9	2·0		R. [illegible]	L. [illegible]
Distance of vulva from tip of tail	—		1·25–1·35		0·55		[illegible]	
Distance between striations of body	—		0·002		[illegible]		[illegible]	
Distance of caudal papillæ (♀) from tip of tail	—		0·27		0·11		0·11	
Size of ova (maximum)	—		—		[illegible]		[illegible]	

spicules are rather slender. Their tips (Pl. VII. fig. 28) are smooth and rather blunt.

The vagina (text-figs. 35, 36) passes into a voluminous uterine sac.

Specific Diagnosis.

ECHINOCEPHALUS MULTIDENTATUS Baylis and Lane.

Head-bulb with 11 to 13 rows of large hooks, each row containing about 100. Dorsal and ventral lobes of lips bear 8 or more teeth each.

TABLE VI.—Hosts and Distribution of the Species of *Echinocephalus*.

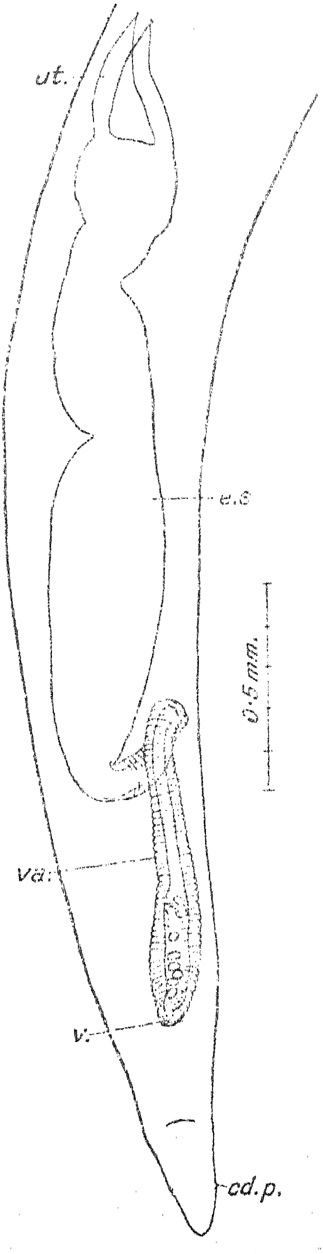
Species.	Host.	Locality.	Recorder.
E. uncinatus (adult)	*Trygon brucco.*	Adriatic.	Molin (1858).
„	*Trygon pastinaca.*	[?]	v. Linstow, in Shipley & Hornell (1904).
(immature)	*Myliobatis nieuhofi.*	Ceylon.	Baylis & Lane (present paper).
„	*Balistes mitis.*	„	Shipley & Hornell (1904).
„	*Balistes stellatus.*	„	„ „
(larva)	*Margaritifera margaritifera.* [*M. vulgaris.*]	„	„ „
„	*Pinna* sp.	„	Baylis & Lane (present paper).
E. spinosissimus......	*Myliobatis aquila.*	Ceylon.	v. Linstow, in Shipley & Hornell (1905).
	Trygon brucco.	Adriatic.	Molin (1858) [recorded as *E. uncinatus*].
	Trygon walga.	Ceylon.	Baylis & Lane (present paper).
	Urogymnus asperrimus.	„	„ „
E. southwelli	*Urogymnus asperrimus.*	Ceylon.	„ „
E. multidentatus ...	*Urogymnus asperrimus.*	Ceylon.	„ „
E. striatus	*Scyllium* sp.	Peru.	Monticelli (1889).
„ (?)	*Aëtobati narinari.*	Loyalty Is.	Shipley (1900).

5. ECHINOCEPHALUS STRIATUS Monticelli, 1889.

Monticelli (1889, p. 71).
? Shipley (1900, p. 560; text-fig. E).

The name *E. striatus* was given by Monticelli to some specimens from the stomach of *Scyllium* sp., from Payta, Peru. Subsequently Shipley doubtfully referred to the same species some

Text-figure 36.



Echinocephalus multidentatus. Posterior end of female; ventral view, showing genital organs.

worms from the intestine of a four-spined sting-ray, *Aëtobatis narinari*, from Loyalty Islands. The name *E. striatus*, however, seems to be a *nomen nudum*, and we have no means of identifying the species, though we mention it here for the sake of completeness. Shipley (*l. c.*) gives a figure of the head of the form referred to by him, and in this figure some 14 rows of hooks are indicated, so that his species would seem to approach closely to our *E. southwelli*, and is possibly identical with it.

GNATHOSTOMA* Owen, 1836.

Gnathostoma Owen (1836, p. 125).
Cheiracanthus Diesing (1838, p. 189).
,, Diesing (1839, p. 221) [not *Cheiracanthus* Diesing of v. Linstow, in Shipley and Hornell (1904, p. 100) nor (1905, p. 54)].
Filaria (in part) Schneider (1866, p. 98).
Cheiranthus v. Linstow (1893, p. 202) [misprint].
Gnathostomum Mitter (1912, p. 150).

The members of this genus are stout worms with the characters of the subfamily. The head-bulb is, according to the state of contraction of the contained muscles, globular or somewhat flattened antero-posteriorly, and bears in the known species from eight to twelve transverse rows of simple hooks, like those of *Echinocephalus*, set on a cuticle which shows no external trace of the four underlying ballonets. Some of the anterior and posterior rows may be obscured, the first by the inrolling of the anterior part of the head-bulb, as the result of contraction of the internal muscles, the second by the partial retraction of the head-bulb into the neck and the resulting interposition of the densely set scale-like spines which cover this part of the body. These are set more or less alternately in transverse rows and have their free edges indented to varying degrees, so that they come to possess sharp points of varying shape and number. Towards the middle of the body the spines become simple and either continue as such to the posterior end or progressively diminish in size and finally disappear, leaving the posterior part of the body naked. The excretory pore has not been detected, a failure easily understood when one considers the dense covering of spines and the minuteness of the pore in other genera of the subfamily.

The male has lateral caudal alæ each sustained by four large papillæ and by the tip of the tail, which has the general appearance of, and has sometimes been counted as, an unpaired terminal papilla (Schneider, 1866, p. 86 and text-fig.; v. Linstow, 1893, p. 206, fig. 11). Between the alæ are two pairs of small, sessile, ventral papillæ. The male has two unequal spicules and no accessory piece, although v. Linstow (1893, p. 206, fig. 13) has described, lying *ventrally* to the spicules, a body which he seems to regard as such, calling it a "Stützapparat."

---

* For generic diagnosis, see p. 292.

The female has a blunt tail: the vulva probably always lies behind the middle of the body; the vagina is long; there are two uteri; the eggs have a thin colourless shell, marked by a very fine external stippling, and have at one pole an appearance as of a watch-glass-shaped cap due to a thinning of the shell combined with a recession of the shell-membrane, and providing a means of exit for the embryo. It has, however, sometimes been described as a polar thickening of the shell (Schneider, 1866, p. 98; v. Linstow, 1893, p. 207).

The genus (*vide* Table VIII., p. 304) has a wide distribution in a number of carnivorous hosts. Its normal habitat is clearly the wall of the stomach. The genotype acquires an added interest in that it has been found in man (in the subcutaneous tissue). The presence of certain species in the lumen of the gut we attribute to their having been parasitic in some host which was devoured by the animals from which they were actually recorded. Regarding one record of a *Gnathostoma* from the colon judgment must be suspended (*vide* p. 305).

Generic Diagnosis.

GNATHOSTOMA* Owen.

Gnathostominæ: head-bulb armed with simple hooks, the ballonets giving no external evidence of their presence; body armed with cuticular spines, anteriorly scale-like with the free edges incised into points varying in number and shape, more posteriorly becoming less subdivided and finally appearing as simple spines, which either continue as such to the posterior end or disappear, leaving the hinder part of the body unarmed; the male with unequal spicules and four pairs of large lateral and two pairs of small ventral caudal papillæ; vulva behind the middle of the body; vagina long; uteri two in number; ovum with thin colourless shell, a marked thinning at one pole causing a weak spot through which the embryo escapes.

Habitat: Normally the gastric wall, usually of carnivorous mammals.

Genotype: *G. spinigerum* Owen, 1836.

NOTE.—The name *Gnathostoma* has been placed on the official list of generic names by the International Commission on Zoological Nomenclature †.

Key to Species of *Gnathostoma*.

A. Body completely clothed with spines .... *G. hispidum* (p. 298).

B. Spines clothe only the anterior half or two-thirds of the body.

  a. The spines immediately behind the head-bulb comb-like, having four points of about equal length...... *G. spinigerum* (p. 293).

---

* For measurements, see Table VII., p. 302.

† Opinion 66 (Smithsonian Institution, Washington).

b. The spines immediately behind the head-bulb leaf-like, having five points, one at the tip and two along either side .... *G. gracile* (p. 300).

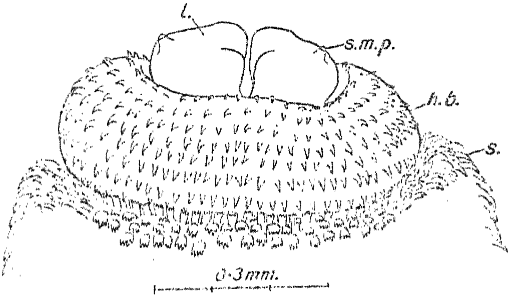
G. horridum and *G. turgidum* are too insufficiently described to be capable of inclusion in a key.

1. GNATHOSTOMA SPINIGERUM * Owen, 1836. (Text-figs. 37–40; Pl. VII. figs. 29–32; Pl. VIII. figs. 33–38).

Gnathostoma spinigerum Owen (1836, p. 125).
Cheiracanthus robustus Diesing (1838, p. 189) [*nomen nudum*].
Cheiracanthus robustus Diesing (1839, p. 222; pl. xiv. figs. 1–7, pl. xvi. figs. 1–24).
Cheiracanthus socialis Leidy (1859, p. 25).
Filaria radula Schneider (1866, p. 98; pl. vi. figs. 9 *a*, 9 *b*).
Cheiracanthus siamensis Levinsen (1889, p. 323; pl. vii. figs. 9–14).
Gnathostoma paronai Porta (1908, p. 8).
Gnathostomum spinigerum Mitter (1912, p. 150; pl. v.).

The contradictory and incomplete character of existing descriptions of this nematode, and the consequent unnecessary multiplication of species, fully justify its redescription.

Text-figure 37.



Gnathostoma spinigerum. Anterior end; dorsal (or ventral) view (surface).

The specimens now described are from *Felis pardus* and were received in part from the Veterinary College, Belgachia, Calcutta, where they were collected by the late Mr. S. N. Mitter, and in part from the Parel Laboratory, Bombay. In each case the worms had produced fatal perforation of the gastric wall.

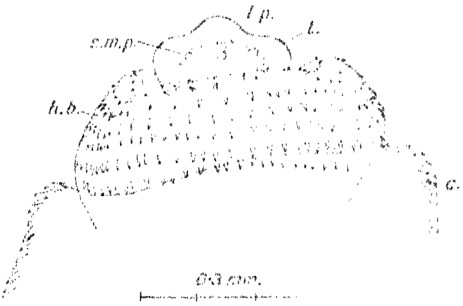
In this species the cuticle lining the inner aspect of each lobe of either lip is longitudinally thickened into a ridge which meets its fellow of the opposite side. In our specimens the head-bulb

---

* For specific diagnosis, see p. 298.

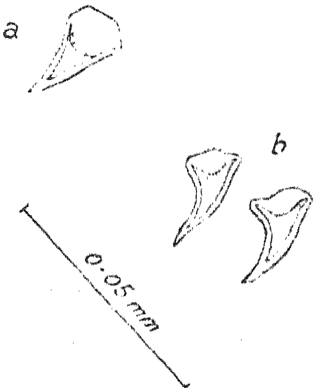
(text-figs. 37, 38; Pl. VII. fig. 23) carries from 8 to 11 rows of hooks (text-fig. 39). The comb-like spines immediately behind the head (text-fig. 40, *a*) carry on their straight distal edges four short points. These rapidly give place to three-pointed spines (text-fig. 40, *b*), the middle point of which is typically the longest. Spines of this type extend posteriorly to beyond the termination

Text-figure 38.



Gnathostoma spinigerum. Anterior end: lateral view (surface).

Text-figure 39.



Gnathostoma spinigerum. Hooks from the head-bulb: *a*, surface; *b*, profile view.

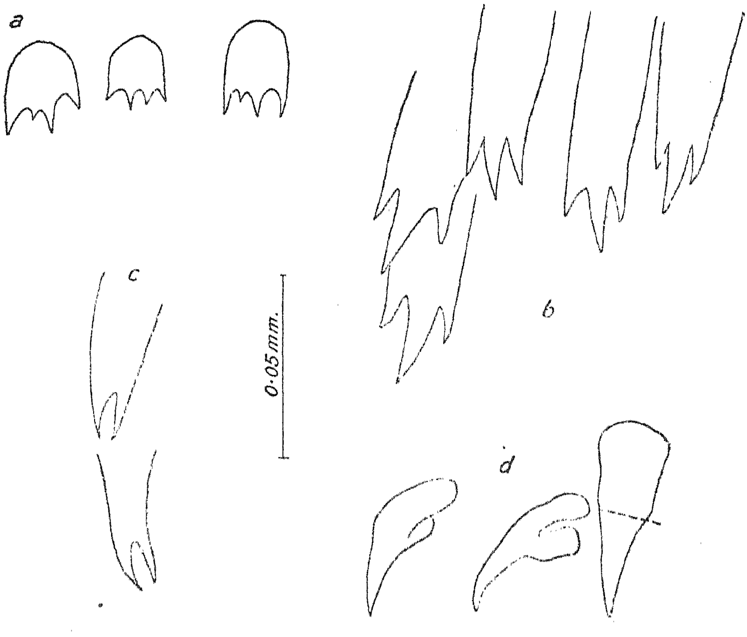
of the œsophagus. There follow progressively two-pointed and single-pointed spines (text-fig. 40, *c*, *d*), which in turn diminish in size so that at 8 mm. from the head-end they form mere points protruding beyond the transverse striations of the cuticle. These soon disappear, leaving the posterior part of the body naked, except for the spines to be described below on the tail of the male.

The diameter of the œsophagus immediately behind the head is 0·125 mm.; its widest diameter is 0·6 mm. and lies at about 0·6 mm. from its termination.

The cervical papillæ (Pl. VII. figs. 30, 31) are coarse, rounded knobs with their terminations directed posteriorly, each lying in a small bald area among the spines.

In the male the four large caudal papillæ on each side (Pl. VII. fig. 32; Pl. VIII. fig. 33) lie close together in the caudal alæ. No. 1 is the smallest, the others being all of about the same size but varying in relative proportions according to the aspect from which they are viewed. Their nerves are particularly large and obvious. Near the bases of Nos. 1 and 2 of these papillæ lie the two pairs of small ventral papillæ. The cloacal opening lies in front of these.

Text-figure 40.



Gnathostoma spinigerum. Body-spines: *a*, from the neck, immediately behind the head-bulb; *b*, from the œsophageal region; *c*, from behind the œsophagus (about 4 mm. from the anterior end); *d*, from about the middle of the body.

On the greater part of the posterior 0·8 mm. of the ventral surface of the caudal extremity the cuticular striæ are closely set with small spines (Pl. VII. fig. 32; Pl. VIII. fig. 33), the general direction of whose points is away from the cloacal opening. There exists, however, a bald Y-shaped area whose narrow stem reaches from the tip of the tail to the anus and whose broad arms stretch thence laterally and anteriorly as far as the most anterior of the lateral papillæ.

The short right spicule (Pl. VIII. fig 34) is wide at the base and narrows somewhat abruptly about its middle, continuing narrow thence to its rounded point. The long left spicule has the same general shape as the right except that the shaft narrows at about the junction of the anterior and middle thirds, and that the middle third has at least the appearance of being the narrowest part. When the large spicule is extruded it is seen that it is hollow-looking, faintly striated, with a fine colourless outer layer which thickens to form the extreme point of a slight terminal expansion (Pl. VIII. fig. 35).

In the female, the vulva, shaped as a slight tranverse slit, opens into a vagina with a general anterior direction. In the specimen examined its first 2 mm. was strongly muscular and narrow, the beginning being markedly tortuous; the next 0·5 mm. was dilated and full of eggs; then followed a narrow muscular loop running posteriorly and dorsally nearly to the level of the vulva and returning on itself to enter another short dilatation close to the first one; thence it ran forward as a narrow muscular tube taking a nearly straight course to the posterior end of the œsophagus. Immediately after turning posteriorly at this point it was found broken and the continuation could not be discovered. The course traced measured 11·5 mm. Owen's (1836, p. 126) account of his dissection gives it a course of over 25 mm. before dividing into the two uteri. The tail of the female is, in a lateral view (Pl. VIII. fig. 37), rounded dorsally and flattened ventrally, while in a ventral view (Pl. VIII. fig. 36) its end is bluntly rounded and carries close to the tip a pair of unusually massive caudal papillæ. It is clear that a collapse of the cuticle about these papillæ might readily produce the "three-lobed" appearance which Levinsen (1889) figures (*vide infra*, p. 297).

The ovum has a thin colourless shell with a very fine granulation on its outer surface and the usual polar cap. In the female examined the ova contained fully-formed embryos, some of which were found in the act of escaping through the thinned pole (Pl. VIII. fig. 38).

The justification for the correctness of the list of synonyms given above is to be sought in the following lines and in Table VII., page 302.

The original description of *Gnathostoma spinigerum* (Owen, 1836) based on specimens removed from tumours in the stomach-wall of a young tiger which died in the London Zoological Gardens, corresponds, so far as details are given, with that just written above, except that he described the armature of the head-bulb as similar to that of the body and noted only one spicule and four pairs of papillæ, apparently three of the large lateral ones and the sessile pair behind the cloacal opening. He found also small worms, possibly young individuals of the same species, 5 lines long *.

Diesing (1839, p. 222) in describing *Cheiracanthus robustus* noted its closeness to *Gnathostoma spinigerum*, but, accepting as correct Owen's description of the head and spicule, he, with diffidence, separated the two forms. It is probably not doubted at the present time that Owen and Diesing were working on the same species. In his subsequent description of Diesing's material, v. Drasche (1883, p. 126) described four pairs of large and three pairs of sessile papillæ.

Under the name of *Cheiracanthus siamensis* Levinsen (1889) described a single poorly preserved immature female nematode which had been removed from an abscess in the breast of a young native woman in Siam. He was able to deal with external characters only. The distribution and shape of the spines on the head and body were identical with those of *Gnathostoma spinigerum*. In his Latin synopsis (*l. c.* p. 325) he uses the expression "*Corpus in partem caudalem trilobatum desinet.*" His figure of the ventral aspect of the tail shows, however, that what actually existed was merely a slight compression of the lateral outline of the tail posteriorly to the anus, a condition which does not correspond to the idea conveyed by the term "three-lobed."

Leiper (1909, p. 70) has described a male of *Gnathostoma siamense* which, as the context indicates, came from a subcutaneous swelling in a native of Siam. The lips were large and fleshy, measuring "1·5 by 0·5 mm." [?0·15 by 0·05 mm.] and each bearing two papillæ with a median protrusion between them. The cephalic hooks measured 0·015 by 0·005 mm. Spines covered the anterior four-fifths of the body, the most anterior having three digitations, the most posterior one only. The ejaculatory duct was 1·5 mm. long. Later Leiper (1911, p. 18; 1913, p. 281), after re-examining Diesing's original examples of *Cheiracanthus robustus* (which, however, he speaks of as having come from the leopard), reaches the conclusion that the male form obtained from man corresponds exactly with the male of *Cheiracanthus robustus*, which, he remarks, "is acceptedly the same as *Gnathostoma spinigerum*." In no respect, indeed, do the forms from the subcutaneous tissue of man differ, except in the matter of maturity, from those from the stomach of Felidæ, but must be considered merely as individuals which have strayed into an unnatural habitat in an unnatural host (*cf.* Leiper, 1909, p. 80).

Cheiracanthus socialis Leidy (1859, p. 53) was found in cavities in the thickened stomach-wall of the mink (*Mustela vison*). There is in its size, in the character of its lips, head and hooks, in the shape and distribution of the spines on the body, in the internal organs, so far as described, and in the genital papillæ, nothing to distinguish it from *Gnathostoma spinigerum*. It does not seem reasonable to consider the name otherwise than as a synonym, pending re-examination of the original material.

---

* Owen did not describe the males as 5 mm. long and the females as twice that length, nor the tail of the female as trilobed (*vide* Stephens, in Fantham, Stephens and Theobald (1916, p. 385)).

Gnathostoma paronai Porta (1908, p. 8) is a name based on a single badly preserved female so opaque that no internal structure was made out. Its meagre description is in every way applicable to *Gnathostoma spinigerum*. It was found free in the intestine of *Rattus* [*Mus*] *rajah*. Its unusual habitat and poor condition suggest that it was in reality a moribund parasite of some animal eaten by the rat.

Schneider (1866, p 98) described from the gastric wall of *Paradoxurus philippinensis* a parasite, *Filaria radula*, with the general external appearance of *Gnathostoma spinigerum*. He also notes particularly that the egg-shell was finely stippled and thickened at one pole, but detected only three pairs of caudal papillæ in the male. He refused to identify his specimens with *Gnathostoma spinigerum*, partly on account of their different geographical distribution and partly because the tail-papillæ, as he believed them to be situated, had an arrangement which he associated with the genus *Filaria*. These reasons for separating it from *G. spinigerum* cannot be accepted as cogent, nor are there any cogent ones to be found in the description.

Specific Diagnosis.

GNATHOSTOMA SPINIGERUM Owen, 1836.

Gnathostoma: eight to eleven rows of hooks on the head-bulb; posteriorly-directed spines cover the anterior half or two-thirds of the body, the anterior being comb-like, with four subequal points, while the three-pointed spines have typically the middle point the longest; in the male, small spines with the points directed away from the cloacal opening cover most of the ventral aspect of the posterior 0·8 mm. of the body; right spicule three or four times as long as the left; tail of the female, in ventral view, uniformly rounded, with very massive papillæ.

For list of hosts, see p. 304.

2. GNATHOSTOMA HISPIDUM [*] Fedchenko, 1872.

Gnathostoma hispidum Fedchenko (1872, p. 106; pl. xv.).

Cheiracanthus hispidus v. Linstow (1893, p. 201; pl. vii. figs. 1–16).

Cheiranthus hispidus v. Linstow (1893, p. 202) [misprint].

The description which follows is based partly on a translation which we have privately obtained of the essential parts of Fedchenko's Russian paper [†], in which he describes material from the wild pig of Turkestan and the domestic pig of Hungary, and partly on descriptions of material from Hungarian pigs by Csokor (1882), v. Rátz (1900), and v. Linstow (1893), and from Roumanian pigs by Ciurea (1911). A paper by Ströse (1892), and one by Collin (1893) in which he claimed to have found this species in the ox in Berlin, we have been unable to consult. The last is of minor importance in that Collin later authorised Wolffhügel (1912) to withdraw this statement, since, in the circumstances under which the material was received, he could not exclude the pig as the possible host. In these descriptions variations from the subfamily and generic characters detailed above (*vide* pp. 254, 291) have, as we believe incorrectly, been described by v. Linstow and Ciurea.

---

[*] For specific diagnosis, see p. 300.

[†] The principal contents of the paper are rendered more accessible through its Latin summary, and through an abstract of it in German by Leuckart (1873).

The anterior body-spines (*vide* Table VII., p. 302) have subequal points, which accordingly, as in *Gnathostoma spinigerum*, terminate at about the same level. More posteriorly the median point tends to become the longest (Fedchenko), the others gradually disappearing, so that at about the posterior end of the œsophagus the spines are simple but long. They extend as such over the rest of the body except, judging by v. Linstow's figures, the large caudal papillæ of the male. Of these there are four pairs, No. 1 being the smallest and separated by an interval from the other three, which lie close together and are of about the same size (Ciurea). Of sessile papillæ Fedchenko figures a pair between the bases of Nos. 1 and 2 of the larger ones; v. Linstow omits these but describes a similar pair close to one another and anterior to the cloacal opening, while Ciurea, in addition to the two pairs which we have described as generic characters, finds three more pairs, two in front of and one behind the cloacal opening. By all these authors the termination of the tail is counted and described as an unpaired median papilla.

The vulva lies in the middle of the body (Fedchenko) or somewhat behind (v. Linstow) or in front of (Csokor, Ciurea) this point. Csokor's description of the œsophagus suggests that the anterior part of his specimens was much contracted, which may explain the anterior position of the vulva in them. We have disregarded these statements in the description of the family. Ciurea and v. Linstow agree in describing the egg as having a hyaline appendage or wart-shaped structure at one pole; the former describes the outer surface of the shell as showing small dimples, the latter finds it smooth. It is stated by v. Linstow that in his specimens embryonic development had begun, and that at the vulva there were a number of many-nucleated cells, which have, however, in his figure an appearance very suggestive of ova.

Except for Collin's statement, later withdrawn, the described habitat (Table VIII., p. 304) has always been the stomach-wall of the pig, penetration into which may be partial or complete, the worms in the latter case (Fedchenko) lying between the gastric tunics.

Specific Diagnosis.

GNATHOSTOMA HISPIDUM Fedchenko, 1872.

Gnathostoma: nine to eleven rows of hooks on the head-bulb; posteriorly directed spines cover the whole of the body, the anterior being comb-like, with seven points, and shorter than the more posterior. The left spicule is twice as long as the right.

For list of hosts, see p. 304.

3. GNATHOSTOMA HORRIDUM (Leidy, 1856).

Cheiracanthus horridus Leidy (1856, p. 53).

Under the name of *Cheiracanthus horridus* Leidy described from the stomach, presumably from the stomach lumen, of *Alligator mississippiensis* four females, $2\frac{3}{4}$ inches long and a line and a half thick, with the body "cylindrical, incurved, posteriorly subclavate, obtuse; anteriorly covered with palmate plates furnished with as many as eight spines and degenerating posteriorly to simple spines." It is uncertain whether this last expression implies that the spines reached the posterior end of the worm.

The want of mention of any burrowing and the fact that the host was a reptile and predatory are in favour of the belief that these worms were really parasites of some host devoured by the alligator; while, with the possible exception of size, there is no characteristic by which this worm can be distinguished from *Gnathostoma hispidum*. Regarding this last point it is probably not disputable that a dead or dying worm commonly increases in size as its muscles relax and decomposition begins.

Gnathostoma hispidum and *G. horridum* are not, however, here described as synonyms, partly because no certain conclusion is possible from the evidence, and partly because to do so would necessitate the substitution of a name based only on females very imperfectly described for one based on specimens which have been investigated with considerable thoroughness. No specific diagnosis of *G. horridum* is attempted.

4. GNATHOSTOMA GRACILE (Diesing, 1838).

Cheiracanthus gracilis Diesing (1838, p. 189), *nomen nudum*.
,, ,, Diesing (1839, p. 225; pl. xiv. figs. 8–11; pl. xvii, figs. 1–20).
,, ,, v. Drasche (1882, p. 126; pl. ix. figs. 1–2).
[Not *Echinocephalus gracilis* Stossich (in Shipley and Hornell, 1906, p. 89).]

Apart from its length (*vide* Table VII. p. 302) this nematode has the following specific characters. The spines on the anterior part of the body are leaf-like, with a maximum of five points, one at the tip and the others along the lateral edges, two on each border. Each cervical sac displays a constriction near its posterior end, a condition, however, which v. Drasche (1882, p. 126) looks upon as a temporary local contraction: the spicules are stouter than in "*Cheiracanthus robustus*"; the four large lateral caudal papillæ of the male are so arranged that there is a considerable interval between Nos. 1 and 2; the egg is figured as being without a polar cap, and the habitat was the intestinal canal of a fish which reaches a length of 15 feet and is presumably carnivorous.

The great length and unusual habitat suggest, as in the case of *Gnathostoma horridum*, that the real host was some mammal which was devoured by the "Pirarucu."

Specific Diagnosis.

GNATHOSTOMA GRACILE (Dies., 1838).

Gnathostoma: anterior body-spines leaf-like, with five points, one at the tip and two along each edge.

5. GNATHOSTOMA TURGIDUM Stossich, 1902.

Gnathostoma turgida Stossich (1902, p. 13).

This species is based on a short description of the external characters of two poorly preserved females. Stossich is convinced that it is distinct from *Gnathostoma spinigerum*, basing his conviction on the statement that the discoidal head-bulb has from 10 to 12 rows of spines, the body is cylindrical and tapers in both directions, and its spines are of varying shape. There is no further information beyond the details to be found in Table VII., p. 302, and Table VIII., p. 304. The name is likely to be a source of future confusion. Since there is nothing specifically distinctive in the description no specific diagnosis is possible.

Species which have been attributed to the Genus *Gnathostoma*.

GNATHOSTOMA SHIPLEYI Stossich, 1900.

Gnathostoma shipleyi Stossich, in Shipley (1900, p. 560, fig. G).
Rictularia paradoxa v. Linstow (1903, p. 272; pl. xviii. fig. 5).
Acuaria pelagica Seurat (1916, p. 785, figs. 1–5).
Seuratia shipleyi Skrjabin (1916, p. 971).

Seurat's careful description of the female of this species discloses neither cervical sacs nor ballonets. The absence of these and of trilobed lips excludes the worm from the Gnathostomidæ.

GNATHOSTOMA PELECANI (Chatin, 1874).

Sclerostoma pelecani Chatin (1874, p. 6; pl. viii. fig. 12; pl. ix. figs. 1, 2).
Gnathostoma pelecani Skrjabin (1916, p. 972).

TABLE VII.—Measurements of

(All measurements

	G. spinigerum.						
Described by	Owen.		Diesing, Dujardin, v. Drasche.	Schneider.	Leidy.		Levinsen.
Under the name of	*Gnathostoma spinigerum.*		*Cheiracanthus robustus.*	*Filaria radula.*	*Gnathostoma sociale.*		*Cheir. siamensis.*
	♂.	♀.			♂.	♀.	♀.
Length	18	25	10 to 12	10 to 12	25	31	9
Thickness (maximum)	2		2·5	2	1	1·15	1
Length of head	...		...	...	...		...
Length of head-bulb	...		...	...	...		...
Transverse diameter of head-bulb	...		...	...	...		...
Length of ballonets	...		...	...	...		...
Distance from head-end to termination of cervical sacs	...		...	...	...		...
Length of neck of cervical sacs	...		...	...	...		...
Breadth of lips	...		...	...	...		...
Number of rows of hooks on head-bulb	6 or 7		6 or 7	...	...		8
Length of hooks on head-bulb	..		...	...	...		...
Breadth of hooks on head-bulb	...		...	...	...		...
Distance between rows of hooks on head-bulb	...		...	...	...		...
Distance between rows of body-spines	...		...	...	...		...
Portion of body covered by spines	anterior two-thirds.						
Maximum number of points on body-spines	3		4	3	3		...
Distance from head-end to cervical papillæ	...		...	...	...		...
Distance from head-end to nerve-ring	...		...	...	...		...
Distance from head-end to termination of œsophagus	...		...	...	...		...
Length of tail	...		...	...	...		...
Length of spicules	...		...	...	...		...
Distance from tip of tail to vulva	8		...	...	...		...
Ova (maximum measurements)	...		...	...	...		...

the Species of *Gnathostoma*.

in millimetres.)

			G. hispidum.						*G. gracile.*	*G. horridum.*	*G. turgidum.*
Leiper.	Baylis & Lane.		v. Linstow.		Csokor.		Ciurea.		Diesing. v. Drasche.	Leidy.	Stossich.
Cheir. siamensis.	*Gnathostoma spinigerum.*										
♂.	♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.			
10·55	16·4 to 16·75	18 to 18·3	15 to 18	22 to 25	25	31	19 to 25	32 to 45	36	65	23
0·6	1·9	1·2	1·18 to 1·38	1·78 to 1·85	2	2·5	...	2·5	2	3	
...	0·4	0·32	...	...	0·37	0·37					
...	0·23	...	0·42								
...	0·55	0·525 to 0·6	0·75								
...	...	0·25									
1	1·8	1·9 to 2·0	0·88		0·7						
...	...	0·3									
"1·5"	0·19 to 0·25	0·2									
8	8 to 11		9 to 11		12		...		...	...	10 to 12
0·015	0·025	...	0·029		0·018						
0·005	0·01	...	...		0·007						
...	0·023										
...	0·017		0·22								
anterior half.	anterior two-thirds.		whole.		...		...		...	...	anterior half.
...	4		7		7		9		5	8	
...	0·7 to 0·75										
...	0·5										
...	3·15 to 3·5	3·4 to 4	1/5·5 of total length.		3·43	5·5					
...	0·22	0·15	...		...		0·312				
R. L.	R.	L.	R.	L.	Longer.	Short'r.					
1·1 0·4	2·3 to 2·63	0·46 0·8	0·4	0·88	1·29	0·32					
...	4		Somewhat behind middle.		Junction of anterior and middle thirds.		In front of middle.				
...	0·06 × 0·035		0·072 × 0·039		...		0·0741 × 0·0418				

Immature forms, 3 mm. long, without sexual organs, were found by Chatin encysted in the subcutaneous tissue, and immature females, not less than 4 mm. long, encysted in the subscapular air-sac, of a pelican (*Pelecanus onocrotalus*). The rounded head showed four transverse rows of hooks. There were six tubes of unequal length, in the position of the cervical sacs. No mention is made of any spines on the body. These features necessitate the provisional inclusion of the species in the Gnathostomidæ, but, if the details are correct, exclude it from any of the genera that we have described.

Table VIII.

Habitat, Hosts and Distribution of the Species of *Gnathostoma*.

Parasite.	Habitat.	Host.	Locality.	Recorder.
G. spinigerum ...	Gastric wall.	*Felis tigris.*	[?]	Owen (1836).
		Felis sylvestris. [*F. catus fer.*]	[?]	Diesing (1839).
		F. catus.	India.	Mitter (1910).
		F. pardus.	"	Mitter (1912).
		"	"	Baylis & Lane (present paper).
		F. concolor.	Brazil.	Diesing (1839).
		Mustela vison.	N. America.	Leidy (1859).
		Paradoxurus philippinensis.	Philippines.	Schneider (1866).
		Canis familiaris.	? Ind	Cobbold (1879).
		" "	India.	Mitter (1912).
	Subcutaneous tissue.	*Homo sapiens.*	Siam.	Levinsen (1899); Leiper (1909).
	Intestine.	*Rattus rajah.*	Island of Mentawei.	Porta (1909).
G. hispidum	Gastric wall.	*Sus scrofa ferus.*	Turkestan.	Fedchenko (1872).
		Sus scrofa domesticus.	Hungary.	" "
		" "	"	v. Linstow (1893).
		" "	"	Czokor (1882).
		" "	"	v. Rátz (1900).
G. horridum.....	Stomach.	*Alligator mississippiensis.*	N. America.	Leidy (1856).
G. gracile........	Intestinal canal.	*Arapaima gigas* [= *Sudis gigas* = *Vastres cuvieri*].	Brazil.	Diesing (1839).
G. turgidum.....	[?]	*Didelphis azaræ.*	Argentine.	Stossich (1902).
Gnathostoma sp.	Wall of large intestine.	*Leontocebus* sp.	French Guiana.	Weinberg & Brimont (1909).

GNATHOSTOMA ACCIPITRI Skrjabin, 1915.

We have been unable to consult a paper in which, under this name, Skrjabin has described a parasite from an eagle in Turkestan. We have no data at all on which to base any comment.

GNATHOSTOMA sp., Weinberg and Brimont, 1909.

These authors give (1909, p. 104) a detailed report on certain lesions produced in the large intestine of a "Tamarin" (a small monkey) in French Guiana by parasites which they identify as Gnathostomes. The habitat induces a natural doubt as to whether the parasites may not have been Œsophagostomes, and a study of the text does not completely dissipate this, since no actual description of the worms is given. The following sentence occurs: "Muni d'un nombre considérable d'épines et de lamelles chitineuses très solides, le Gnathostome enfonce profondément son extrémité céphalique, et peut ainsi amener, par ce seul moyen mécanique, une rupture de la paroi intestinale." It is not clear whether the expressions used here refer to Gnathostomes in general or to these worms in particular, so that it appears wise to suspend judgment as to the systematic position of these parasites till they have been properly described.

For *Cheiracanthus uncinatus* and *Cheiracanthus spinosissimus* see *Echinocephalus* (*supra*, p. 273), to which genus they belong.

Genera doubtfully to be attributed to the Gnathostomidæ.

ANCYRACANTHUS Diesing, 1839.

Ancyracanthus Diesing (1839, p. 227).
Ancryacanthus v. Linstow (1893, p. 205).
Genotype: *Ancyracanthus pinnatifidus* Diesing (1839, p. 227; pl. xiv, figs 21–27; pl. xviii. figs. 1–20).
Ancyracanthus pinnatifidus v. Drasche (1884, p. 111; pl. iv. figs. 6–11).

These nematodes are characterized by the fact that the head bears four appendages set cross-wise, two springing from each of the lateral lips. Each appendage is pinnate and is connected with a cervical sac. Furthermore, from the attachment between appendage and sac springs a long conical process, nearly as long as and lying close beside the latter. Diesing and von Drasche are in disagreement regarding the existence of a communication between the cavities of the sac and of the appendage, which, taking into consideration the complicated branching character of the latter, is not surprising. It is stated by von Drasche that the cervical sacs have no spiral layer.

Habitat: gut of *Podocnemis expansa* and *P. tracaxa*.

ELAPHOCEPHALUS Molin, 1860.

Elaphocephalus Molin (1860, p. 343).
Genotype: *Elaphocephalus octocornutus* Molin (1860, p. 344).
" " v. Drasche (1884, p. 113; pl. iii. figs. 21–23).

This genus and species, based on a single female from *Ara* [*Psittacus*] *macao*, are characterized by the possession of four cervical sacs which are without the internal processes found in *Ancyracanthus*. As in that genus, there are four freely-projecting external appendages, each of which, however, possesses an external process shorter than itself. The cuticle of the body carries closely-set spines.

Whether *Ancyracanthus pinnatifidus* and *Elaphocephalus octocornutus* do or do not belong to the Gnathostomidæ can only be ascertained after further investigation, but it is not impossible that the structures just mentioned correspond to the ballonets and cervical sacs of the *Gnathostominæ*. If this be so, the difference between the subfamily and these two forms presumably lies in an exuberant development, in the latter, of the ballonets, unconfined by a stout overlying covering. In the forms unquestionably belonging to the subfamily such confinement within a uniform head-bulb is complete in *Gnathostoma* and *Echinocephalus*, less complete in *Tanqua anomala* and *T. diadema*, and least so in *Tanqua tiara*, in which last the prominences corresponding to the four underlying ballonets are sometimes strikingly distinct. It is not difficult to imagine that further exuberance and external subdivision or indentation of the cuticle covering the ballonets might well produce those external and internal modifications which have been described in these two genera.

NOTE.

Our best thanks are due to Mr. T. Southwell, formerly Director of Fisheries for Bengal, Bihar and Orissa, for supplying us with much of the material upon which the work has been based, especially as regards the genus *Echinocephalus*.

As regards the nomenclature of the hosts, we are indebted to Mr. Oldfield Thomas, F.R.S., for verifying and correcting the names of all the mammals mentioned in the paper; and to Mr. C. Chubb, Dr. G. A. Boulenger, F.R.S., and Mr. C. Tate Regan, F.R.S., for performing the same kind office in the cases of birds, reptiles, and fishes respectively.

For the preparation of some excellent serial sections we are indebted to the skill of Mr. Cecil Gunns, of the Zoological Department, Imperial College of Science.

For all errors and omissions we accept full responsibility.

The figures have all been drawn to scale with the aid of the Abbé camera lucida.

The type-specimens of the species described as new are in the British Museum (Natural History).

REFERENCES.

(Works not seen by the authors are marked with an asterisk.)

BAYLIS, H. A. (1916)—The Nematode Genus *Tanqua*, R. Blanchard. Ann. & Mag. Nat. Hist. (8) xvii. pp. 223-232.

BLANCHARD, R. (1904)—*Tanqua*, n.g., remplaçant *Ctenocephalus* von Linstow. Arch. Parasitol., Paris, viii. p. 478.

CHATIN, J. (1874)—Études sur des Helminthes nouveaux ou peu connus. Ann. Sci. Nat., Paris, (6) Zoologie, i., Art. 6, pp. 1-18 (separately paged), pls. viii.-ix.

CIUREA, J. (1911)—Über *Gnathostoma hispidum* Fedtsch. Zeits. Infekt.-krankh. Haustliere, Berlin, x. pp. 288-292; 1 pl.

COBBOLD, T. S. (1864)—Entozoa. London.

„ „ (1879)—Parasites; a Treatise on the Entozoa of Man and Animals. London.

*COLLIN, —— (1893)—Notiz über *Gnathostoma hispidum* Fedtsch. aus dem Rinde. Zs. f. Fleisch- u. Milchhyg., iii. p. 119.

CSOKOR, J. (1882)—*Gnathostoma hispidum* suis s. *Cheiracanthus* Diesing. Österr. Vierteljahrs. f. Wiss. Veterinärk. lvii. pp. 1-22; 1 pl.

DIESING, K. M. (1838)—Bericht über die XV. Versamml. deutsch. Naturf. u. Aerzte, (Prag) p. 189.

„ „ (1839)—Neue Gattungen von Binnenwürmern. Ann. Wien. Mus. (1840), pp. 219-242, pls. xiv.-xx.

„ „ (1861)—Revision der Nematoden. Sitz. k. Akad. Wiss. Wien, xlii. pp. 595-736; 1 pl.

DRASCHE, R. VON. (1883)—Revision der in der Nematoden-Sammlung des k.-k. zool. Hofcabinetes befindl. Original-Exemplare Diesing's und Molin's. Verh. k.-k. zool.-bot. Ges., Wien, xxxii. pp. 117-138, pls. vii.-x.

„ „ (1884)—*Idem.* *Ib.* xxxiii. pp. 107-118, pls. iii.-v.

FANTHAM, H. B.; STEPHENS, J. W. W.; and THEOBALD, F. W. (1916)—The Animal Parasites of Man. London.

FEDCHENKO, A. P. (1872)—Zoologitjeskija Samjetki. Trans. Soc. Nat. Moscow, x. pp. 100-111, pls. xiv.-xv. (Russ.)

HALL, M. C. (1916)—Nematode Parasites of Mammals of the orders Rodentia, Lagomorpha, and Hyracoidea. Proc. U.S. Nat. Mus., Washington, L., pp. 1-258.

*HUBER, J. C. (1898)—Bibliographie der klinische Helminthologie, Supplementheft. Jena.

JÄGERSKIÖLD, L. A. (1909)—Nematoden aus Ägypten und dem Sudan. Swed. Zool. Exp. Egypt & White Nile, 1901, Part III. pp. 1-56 + v; 4 pls.

LEIDY, J. (1856)—A Synopsis of Entozoa and some of their Ectocongeners. Proc. Acad. Nat. Sci., Philad., pp. 42-58.

„ „ (1859)—Proc. Biol. Dept., Ac. Nat. Sci.; in: Proc. Ac. Nat. Sci., Philad., 1858 (pub. 1859), [separately paged, and bound at end of vol.], p. 25.

LEIPER, R. T. (1908)—An account of some Helminthes contained in Dr. C. M. Wenyon's Collection from the Sudan. Rep. Wellcome Res. Lab., Khartoum, iii. pp. 187-199; (published 1909).

„ „ (1909)—The Structure and Relationships of *Gnathostoma siamense* (Levinsen). Parasitology, Cambridge, ii. pp. 77-80.

LEIPER, R. T. (1911)—Notes on recent and some new records of Helminthes of Man of which there are few records. Journ. London Sch. Trop. Med., Part I. pp. 16–19.

" " (1913)—Observations on certain Helminths of Man. Trans. Soc. Trop. Med. & Hyg., vi., 8., pp. 265–297.

LEUCKART, R. (1873)—Bericht über die wiss. Naturg. der niederen Thieren, 1872–1875. Arch. f. Naturg., Berlin, xxxix. pp. 560–561.

LEVINSEN, G. M. R. (1889)—Om en ny Rundorm hos Mennesket, *Cheiracanthus siamensis*, nov. sp. Vidensk. Meddel. Naturh. For., Kjöbenhavn (1890), pp. 323–326, pl. vii. figs. 9–14.
Abstract in German by H. Krabbe in Centralbl. f. Bakt. u. Parasit., Jena, viii. p. 182 (1890).

LINSTOW, O. VON. (1879)—Helminthologische Untersuchungen. Württemb. Naturw. Jahresh. xxxv. pp. 313–342, pl. v.

" " (1893)—*Oxyuris paronai* n. sp. und *Cheiracanthus hispidus* Fedt. Arch. f. Naturg., Berlin, lix., 1., pp. 201–208, pl. vii. figs. 1–16.

" " (1903)—Entozoa des Zool. Mus. der k. Akad. Wiss. zu St. Petersburg. II. Ann. Mus. Zool. Ac. Imp. Sci., St. Petersburg, viii. 3–4., pp. 265–294, pls. xvii.–xix.

" " (1904 *a*)—Nematoda in the Collection of the Colombo Museum. Spolia Zeylanica, i. pp. 91–104, pls. i.–ii.

" " (1904 *b*)—Beobachtungen an Nematoden und Cestoden. Arch. f. Naturg., Berlin, lxx., 1., pp. 297–309, pl. xiii.

" " (1906)—Helminthes from the Collection of the Colombo Museum. Spolia Zeylanica, iii., 11., pp. 163–188, pls. i.–iii.

" " (1909)—Parasitische Nematoden: in Brauer, Die Süsswasserfauna Deutschlands, Jena, Heft 15, pp. 47–92.

MITTER, S. N. (1910)—*Gnathostoma spinigerum* in a domestic Cat. Journ. Trop. Vet. Sci., Calcutta, pp. 284–285, pl. xxiv.

" " (1912)—Note on *Gnathostomum spinigerum*. Parasitology, Cambridge, v., 2., p. 150, pl. v.

MOLIN, R. (1858)—Prospectus helminthum, quæ in prodromo faunæ helminthol. Venetiæ continentur. Sitz. k. Akad. Wiss., Wien, xxx. pp. 127–158.

" " (1860)—Trenta specie di Nematoidi. Sitz. k. Akad. Wiss., Wien, xl. pp. 331–358.

" " (1861)—Prodromus Faunæ Helminthologicæ Venetæ. Denk. k. Akad. Wiss., Wien, xix. pp. 189–338, pls. i.–xv.

MONTICELLI, F. S. (1889)—Elenco degli Elminti raccolti dal Capitano G. Chierchia durante il viaggio . . . della R. corvetta "Vettor Pisani." Boll. Soc. Nat., Napoli, (1) iii. pp. 67–71.

OWEN, R. (1836)—Proc. Zool. Soc., London, Part IV. pp. 123–126.

PARONA, C. (1898)—Elminti raccolti dal Dott. Elio Modigliani alle isole Mentawei, Engano e Sumatra. Ann. Mus. Genova, (2) xix. pp. 102–124, pl. i.

PORTA, A. (1908)—Descrizione di una nuova specie di Gnathostomidæ (Nematodes). Zool. Anz., Leipzig, xxxiii. pp. 8–9.

Railliet, A. (1895)—Traité de Zoologie médicale et agricole. Paris.

Railliet, A., & Henry, A. (1916)—Sur les Oxyuridés. C. R. Soc. Biol., Paris, lxxix. pp. 113–115.

Rátz, S. von. (1900)—Neue Nematoden in der Ungarischen Fauna. Termész. Füzetek, xxiii. pp. 178–186, pl. v.

Rudolphi, C. A. (1809)—Entozoorum Historia Naturalis. Amsterdam, ii., Part I.

„ „ (1819)—Entozoorum Synopsis. Berlin.

Schneider, A. (1866)—Monographie der Nematoden. Berlin.

*Schneider, J. G. (1789)—Naturgeschichte der Schildkröten. Zweyte Beytrag.

Seurat, L.-G. (1915)—Expédition de MM. Walter Rothschild, E. Hartert et C. Hilgert dans le Sud Algérien (Mars–Mai 1914). Nématodes Parasites. Novitates Zoologicae (Tring), xxii. pp. 1–25.

„ „ (1916)—Sur un nouveau Dispharage des Palmipèdes. C. R. Soc. Biol., Paris, lxxix. pp. 785–788.

„ „ (1918)—Nématodes de la Clemmyde lépreuse. Bull. Soc. Hist. Nat. Afrique Nord, ix., 1., pp. 20–26.

Shipley, A. E. (1900)—A Description of the Entozoa collected by Dr. Willey during his Sojourn in the Western Pacific; in: Willey, A., 'Zoological Results' (Cambridge), Part V. pp. 531–568, pls. liv.–lvi.

Shipley, A. E., & Hornell, J. (1904)—The Parasites of the Pearl Oyster; in: Herdman, W. A., Roy. Soc. Rep. Pearl Fisheries, Part II. pp. 77–106, pls. i.–iv.

Shipley, A. E., & Hornell, J. (1905)—Further Report on Parasites found in connection with the Pearl Oyster Fishery at Ceylon. *Ib.*, Part III. pp. 49–56; 1 pl.

Shipley, A. E., & Hornell, J. (1906)—Report on the Cestode and Nematode Parasites from the Marine Fisheries of Ceylon. *Ib.*, Part V. pp. 43–96; pls. i.–vi.

*Skrjabin, K. J. (1915)—Nématodes des oiseaux du Turkestan russe. Ann. Mus. Zool. Ac. Imp. Sci., Petrograd, xx. pp. 534–535.

Skrjabin, K. J. (1916)—*Seuratia*, n. g., nouveau genre de Nématodes d'oiseaux. C. R. Soc. Biol., Paris, lxxix. pp. 971–973.

Stiles, C. W., & Hassall, A. (1905)—The Determination of Generic Types. Bull. Bur. Anim. Indust., U.S. Dept. of Agric., Washington, No. 79.

Stossich, M. (1896)—Il Genere *Ascaris* Linné. Boll. Soc. Adriat. Sci. Nat., Trieste, xvii. pp. 9–113.

„ „ (1902)—Sopra alcuni Nematodi della Collezione elmintologica del Prof. Dott. Corrado Parona. Boll. Mus. Zool. e Anat. Comp., R. Univ. Genova, No. 116, pp. 1–16, pls. iii.–v.

*Ströse, A. (1892)—Magenwurmseuche bei Schweinen hervorgerufen durch *Cheiracanthus hispidus*. Berliner thierärztl. Wochenschr. xlvii. p. 552.

Wedl, K. (1862)—Zur Helminthenfauna Ägyptens, II. Sitz. k. Akad. Wiss. Wien, xliv., Abth. 1., pp. 463–482, pls. i.–iii.

Weinberg, M., & Brimont, E. (1909)—Lésions de l'Intestin produites par le *Gnathostome*. Bull. Soc. Path. exot., Paris, ii. pp. 104–105; 1 pl.

Wolffhügel, K. (1912)—*Gnathostoma hispidum* Fedtsch. ist kein Parasit von *Bos taurus*. Bemerkung zu der Arbeit von J. Ciurea. Zeits. Infekt.-krankh. Hausthiere, Berlin, xi. p. 65.

Explanation of Lettering of Text-figures and Plates.

a., button-like appendage of cervical sac.
b., ballonet.
b.c., cavity of ballonet.
c., collar.
c.p., cervical papilla.
c.s., cervical sac.
c.s.n., neck of cervical sac.
c.t., cuticular thickening.
cd.p., caudal papilla.
e.p., excretory pore.
e.s., egg-sac.
h., hooks.
h.b., head-bulb.
h.m., head-muscle.
l., lip.
l.p., lateral papilla.
l.p.n., nerve of lateral papilla.
n.r., nerve-ring.
œs., œsophagus.
r.g., rectal glands.
s., spines.
ser., serrations.
s.m.p., submedian papilla.
s.m.p.n., nerve of submedian papilla.
sp., spicule.
su., sucker-like depression.
t., *t.*, teeth.
tl., termination of tail.
ut., uterus.
v., vulva.
va., vagina.

EXPLANATION OF PLATES I.–VIII.

Fig. 1.	*Spiroxys contorta.*	The head; dorsal (or ventral) view.
2.	,, ,,	The head; lateral view.
3.	,, ,,	Tail of male; ventral view. (Right spicule broken).
4.	,, ,,	Tail of male; lateral view.
5.	,, ,,	Tail of male; lateral view, at a higher magnification, to show the papillæ.
6.	*Spiroxys gangetica.*	The head; dorsal (or ventral) view.
7.	,, ,,	The head; lateral view.
8.	,, ,,	Caudal extremity of male; ventral view.
9.	,, ,,	Caudal extremity of male; lateral view.
10.	,, ,,	Terminal portion of spicule.
11.	*Tanqua tiara.*	The head; nearly dorsal view.
12.	,, ,,	Tail of male; ventral view.
13.	,, ,,	Tail of male; lateral view.
14.	*Tanqua anomala.*	Tail of male; lateral view.
15.	*Tanqua diadema.*	Tail of male; ventral view.
16.	,, ,,	Tail of male; lateral view.
17.	*Echinocephalus spinosissimus.*	Tail of male; nearly ventral view.
18.	,, ,,	Terminal portion of spicule.
19.	*Echinocephalus southwelli.*	The lips; dorsal (or ventral) view.
20.	,, ,,	One of the lips; lateral view. The cuticular thickenings are seen by transparency.
21.	,, ,,	Tail of male; ventral view.
22.	,, ,,	Tail of male; lateral view.
23.	,, ,,	Terminal portion of spicule.
24.	*Echinocephalus multidentatus.*	The lips; dorsal (or ventral) view.
25.	,, ,,	One of the lips; lateral view. The teeth are seen by transparency.
26.	,, ,,	Tail of male; ventral view.
27.	,, ,,	Tail of male; lateral view.
28.	,, ,,	Terminal portion of spicule.
29.	*Gnathostoma spinigerum.*	Anterior end: lateral view (optical section).
30.	,, ,,	Surface view of one of the cervical papillæ, surrounded by spines.
31.	,, ,,	Profile view of one of the cervical papillæ.
32.	,, ,,	Tail of male; ventral view. On the left-hand side of the drawing most of the spines have been omitted.
33.	,, ,,	Tail of male; lateral view.
34.	,, ,,	The spicules.
35.	,, ,,	Terminal portion of left spicule.
36.	,, ,,	Tail of female; ventral view.
37.	,, ,,	Tail of female; lateral view.
38.	,, ,,	Ova, some with embryos escaping.

17. Contributions to a Study of the Dragonfly Fauna of Borneo.—Part IV. A List of Species known to occur in the Island. By F. F. LAIDLAW, M.A.(Cantab.), F.Z.S.

[Received April 9, 1920: Read April 27, 1920.]

(Text-figures 1–4.)

INDEX.

	Page
I. Introduction	311
II. List of Species	312
III. Some Remarks on Geographical Distribution	341

I. *Introduction.*

I have attempted in the following list to catalogue all species of Dragonflies which have been recorded from Borneo, or which are otherwise known to me to occur in the island.

In the case of some species I have added notes that may, I hope, be of service to others who may deal with this fauna.

In addition to records already available in the literature of the order Odonata, I have been able to compile my list from the examination of the large amount of material sent me by Major J. C. Moulton whilst Curator of the Sarawak Museum. Some of this material has already been dealt with, as noted in the references to literature; and Major Moulton's type specimens are, unless otherwise noted, deposited in the British Museum. Where possible, paratypes have been sent to the Sarawak Museum.

I have also been able to examine a collection sent to me nearly twenty years ago by Dr. C. Hose from the Baram district.

References to specimens examined deal in every case with Major Moulton's material unless otherwise stated.

His localities are in the territory of Sarawak, with the following exceptions, which are in British North Borneo:—Mt. Kinabalu, Tampassuk (River), and Khotabelud.

In order to avoid undue prolixity in the list, I have given references chiefly, if not entirely, to faunistic and systematic papers. For the *Libellulinæ* I have thought it necessary to quote only Dr. Ris's Monograph of the subfamily, referred to in the sequel as "Ris, Cat. Coll. Selys, Libell." ('Catalogue Systématique et Descript. Collections Zoologiques du Baron Edm. de Selys-Longchamps,' Fasc. ix.–xvi., Libellulinæ). The publication of the Monograph was completed in 1919, and it contains a very full synonymy of all the Bornean species.

For the *Gomphinæ* and *Chlorogomphinæ* I give reference only to my previous paper on the group (these Proceedings, 1914, pp. 51–63, pl. i.), where citations of recent papers are to be found.

For species of other groups I quote, where available, Kirby's 'Synonymic Catalogue of Neuroptera Odonata' (1890) as "Kirby, Cat. Odonata," and, in addition, references to later papers. Of these, Fasc. xvii. of the 'Catalogue of Collections du Baron Edm. de Selys-Longchamps,' dealing with the Cordulinæ, by Martin, is referred to as "Martin, Cat. Coll. Selys, Cordul."; whilst Fasc. xviii.–xx. of the same Catalogue, dealing with the Æschninæ, are referred to as "Martin, Cat. Coll. Selys, Æschn."

I have in certain cases given measurements of the specimens noted, in each case of the abdomen "abd." and hinder-wing "h. w." In the case of the male, after the measurement of the abdomen, the sign + followed by another measurement refers to the length of the anal appendages.

Where the venation of the wings is discussed, I have used the revised nomenclature proposed by Tillyard in his book, 'The Biology of Dragonflies.'

An asterisk placed before the name of a species signifies that I have not seen a specimen of that species from Borneo.

Parentheses around the names of authors placed after specific names in this paper are used in accordance with Article 23 of the International Rules of Nomenclature (Proc. 7th Int. Cong. Boston, 1907, p. 44 (1912)).

II. *List of Species.*

ANISOPTERA.

ÆSCHNIDÆ.

CHLOROGOMPHINÆ.

1. OROGOMPHUS DYAK Laidlaw.

Orogomphus dyak Laidlaw, Proc. Zool. Soc. London, 1914, pp. 59–60, pl. i. figs. 4–7.

2 ♂♂, 2 ♀♀. Mt. Matang. 3 ♂♂. Mt. Merinjak, 2200 ft., 28. v. 14.

2. OROGOMPHUS SPLENDIDUS Selys.

Orogomphus splendidus Laidlaw, Proc. Zool. Soc. London, 1914, pp. 60–61, pl. i. fig. 8.

2 ♀♀. Sarawak.

ÆSCHNINÆ.

3. *LINÆSCHNA POLLI Martin.

Linæschna polli Martin, Cat. Coll. Selys, Æschn. pp. 136–137, (figs. 133, 134), pl. iii. fig. 9.

4. JAGORIA MODIGLIANII (Selys).

Oligoæschna modiglianii Kirby, Cat. Odonata, p. 86.

Doleschna elacatura Needham, Bull. Amer. Mus. Nat. Hist. 23, p. 143, fig. 3.

? *Jagoria pœciloptera* (pars) Karsch, Entom. Nachr. xv. p. 239 (♂).

Jagoria elacatura Martin, Cat. Coll. Selys, Æschn. p. 135.

Jagoria modiglianii Krüger, Stettin. Entomol. Zeitg. 1898, pp. 238–259, 327; Martin, Cat. Coll. Selys, Æschn. p. 130 (figs. 126, 127); Ris, Ann. Soc. Entomol. Belg. pp. 240–242.

2 ♀ ♀. Matang Rd.

I have followed Ris in the synonymy of this species.

Wings suffused with golden brown throughout.

♀. Abd. 40 mm., h. w. 42 mm.

5. *JAGORIA PŒCILOPTERA Karsch.

Jagonia pœciloptera Karsch, Entom. Nachr. xv. 1889, p. 238; Krüger, Stettin. Entomol. Zeitg. 1898, pp. 327–328; Martin, Cat. Coll. Selys, Æschn. pp. 132–133 (fig. 129).

6. *JAGORIA BUHRI Förster.

Jagoria buhri Förster, Insecten-Börse, 1903; Martin, Cat. Coll. Selys, Æschn. pp. 131–132 (fig. 128).

This species recorded from N. Borneo by Dr. Förster appears to me to be very closely related to that immediately preceding it. I have not seen examples of either of these two last species.

7. HELLÆSCHNA IDÆ (Brauer).

Amphiæschna? *idæ* Kirby, Cat. Odonata, p. 93.

Heliæschna idæ Krüger, Stettin. Entomol. Zeitzg. 1898, pp. 323–324; Martin, Cat. Coll. Selys, Æschn. pp. 164–165 (fig. 166); Ris, Ann. Soc. Entomol. Belg. lv. 1911, pp. 242–243 (fig. 10).

1 ♂. Matang Rd., 2. ii. 11. 1 ♂. Kuching, 4. ii. 98. 1 ♂. Buntal, iii. 12. 1 ♀. Matang Rd., 4. i. 11. 1 ♀. Saribas, xi. 1900. 1 ♀. Kuching, iv. 03.

♂. Abd. 52 + 7 mm., h. w. 52 mm. ♀. Abd. 57 + mm., h. w. 53 mm.

The females each have four large spines on ventral plate, the median pair being larger than the lateral pair. The apex of the plate is strongly decurved, and the margin carries smaller spines on either side of the four larger ones. From the description and figures (Martin, *loc. cit.* figs. 163, 166) I cannot separate this species from the next.

8. *HELIÆSCHNA CRASSA Krüger.

Heliæschna crassa Krüger, Stettin. Entomol. Zeitg. 1898, pp. 324–325; Martin, Cat. Coll. Selys, Æschn. pp. 162–163 (fig. 163).

9. *HELIÆSCHNA UNINERVULATA Martin.

Heliæschna uninervulata Martin, Cat. Coll. Selys, Æschn. pp. 163–164 (figs. 165, 168).

This species, described originally from Borneo, occurs also in Lower Burma. (1 ♂, coll. E. B. Williamson.)

10. *HELIÆSCHNA SIMPLICIA (Karsch).

Amphiæschna simplicia Karsch, Ent. Nachr. xvii. 1891, p. 308; Karsch, Ent. Nachr. xviii. 1892, p. 250.

Heliæschna simplicia Karsch, Ent. Nachr. xix. 1893, p. 195; Martin, Cat. Coll. Selys, Æschn. pp. 161–162 (fig. 162).

11. *AMPHIÆSCHNA PERAMPLA Martin.

Amphiæschna perampla Martin, Cat. Coll. Selys, Æschn. p. 115 (figs. 108, 109).

12. AMPHIÆSCHNA GRUBAUERI Förster.

Amphiæschna grubaueri Förster, Insekten-Börse, xxi. (1904) pp. 1–3 (sep.); Martin, Cat. Coll. Selys, Æschn. pp. 115–116 (fig. 110); Laidlaw, Journ. Straits Branch R. Asiat. Soc. lxiii. 1912, p. 94.

1 ♀. Mt. Batu Lawi, 24. v. 11.

The arculus in the fore-wings of this specimen is of a primitive character. The upper part is very oblique and readily seen to be formed by M_{1-3}, M_1, which separate before M_4 is met by the scarcely thickened cross-vein which forms the lower part.

The upper part of the hinder-wing is much less oblique.

The costal, subcostal, median, and cubito-anal spaces in both fore- and hinder-wing are opaque, dark brown to a level of about one cell before the arculus; the anal area of both wings tinged with orange-brown to about the same level. Beyond the nodus the wings are tinged with orange-brown almost to the apex.

The ventral plate curves upwards at its apex and carries about 8 small irregular spines. Its ventral surface has a deep conical depression to receive the points of the terebræ.

Abd. 62 mm., h. w. 63 mm. Pt. 2 mm.

(The measurement given by me (*loc. cit.*) of 70 mm. for the hinder-wing was an error.)

13. TETRACANTHAGYNA PLAGIATA (Waterhouse).

Tetracanthagyna plagiata Kirby, Cat. Odonata, p. 94; Krüger, Stettin. Entomol. Zeitg. 1898, pp. 287–288; Martin, Cat. Coll. Selys, Æschn. pp. 145–146 (figs. 144, 145).

1 ♀. Kakus, vi. 13.

Ris (*loc. cit.*) suggests that the next species, separated from *plagiata* on account of the colouring of the wings of the female, is identical with it; and that *T. plagiata* has two forms of female, one with a costal stripe and transverse band of brown on the wings

(*T. plagiata* type), the other with costal stripe only (*T. vittata* type). No male with transverse bands has been recorded. Structurally the females of the two forms are identical, and Ris's view is in all probability correct. In this case *T. vittata* McLach. will be a synonym of *T. plagiata* Waterh.

♀. Abd. 68 mm., h. w. 80 mm.

[TETRACANTHAGYNA VITTATA McLach.]

Tetracanthagyna vittata McLachlan, Trans. Entomol. Soc. London, 1898; Martin, Cat. Coll. Selys, Æschn. pp. 144–145 (fig. 143); Ris, Ann. Soc. Entomol. Belg. lv. 1911, pp. 243–244.

1 ♂, 1 ♀. Kuching, iv. 99.

See remarks under *T. plagiata*.

The female of this pair is possibly the largest and bulkiest individual of all living Odonata on record. The pair in full flight must have afforded a splendid sight to any entomological enthusiast.

♂. Abd. 70+7·5 mm., h. w. 72 mm.

♀. Abd. 70 mm., h. w. 83 mm.

14. *TETRACANTHAGYNA DEGORSI Martin.

Tetracanthagyna degorsi Martin, Bull. Soc. Entom. France, 1895; McLachlan, Trans. Entomol. Soc. London, 1898; Krüger, Stettin. Entomol. Zeitg. 1898, p. 288; Martin, Cat. Coll. Selys, Æschn. p. 147.

15. *TETRACANTHYGNA WATERHOUSEI McLach.

Tetracanthagyna waterhousei McLachlan, Trans. Entomol. Soc. London, 1898: Martin, Mission Pavie, Névroptères, (sep.) p. 14; Martin, Cat. Coll. Selys, Æschn. pp. 143–144 (fig. 142).

16. TETRACANTHAGYNA BRUNNEA McLach.

Tetracanthagyna brunnea McLachlan, Trans. Entomol. Soc. London, 1898; Martin, Cat. Coll. Selys, Æschn. pp. 146–147 (fig. 141).

Tetracanthagyna plagiata Laidlaw (nec Waterhouse), Proc. Zool. Soc. London, 1902, p. 79.

(The specimen recorded by me, *loc. cit.* 1902, from the Malay Peninsula belongs here and not to *T. plagiata*.)

1 ♀. Sarawak: h. w. 66 mm., abd. 55 mm.

17. GYNACANTHA DEMETER Ris.

Gynacantha demeter Ris, Ann. Soc. Entomol. Belg. lv. 1911. pp. 245–246 (fig. 12).

1 ♂, 1 ♀. Matang Rd., 22. ii. 20.

18. GYNACANTHA DOHRNI Krüger.

Gynacantha dohrni, Krüger, Stettin. Entomol. Zeitg. 1898, pp. 277–287, fig. p. 280; Martin, Cat. Coll. Selys, Æschn.

pp. 199–200 (fig. 204); Ris, Ann. Soc. Entomol. Belg. lv. 1911, pp. 244–246 (fig. 11).

2 ♂ ♂. Saribas. 1 ♂. Quop, 19. iii. 14. 1 ♀. Mt. Merinjak, 23. v. 14. 2 ♀ ♀. Matang Rd., 1. iv. 12. 1 ♀. Kuching, 14. i. 96.

The collection also contains 3 ♀ ♀ which I have not been able to identify with certainty. They are from Tabekang, 13. v. 14, and Kakus, vi. 1913. In these specimens the wings are suffused with orange-brown. The material at my disposal is unfortunately insufficient to permit a satisfactory handling of the genus.

19. *GYNACANTHA BASIGUTTATA Selys.

Acanthagyna basiguttata Kirby, Cat. Odonata, p. 95.

Gynacantha basiguttata Krüger, Stettin. Entomol. Zeitg. 1898, pp. 277–284, fig. p. 279; Martin, Mission Pavie, Névroptères, (sep.) p. 14; id., Cat. Coll. Selys, Æschn. pp. 192–193 (fig. 197); [? fig. 197 = *G. dohrni* Krüger, see Ris, *loc. cit.*]; Ris, Ann. Soc. Entomol. Belg. lv. 1911, pp. 246–247 (fig. 13).

20. *GYNACANTHA BAYADERA Selys.

Gynacantha bayadera Selys, Ann Mus. Civ. Genova 2. x. (xxx.) 1890, p. 51; Krüger, Stettin. Entomol. Zeitg. 1898, pp. 277–283, fig. p. 280; Martin, Mission Pavie, Névroptères, (sep.) p. 14; Martin, Cat. Coll. Selys, Æschn. pp. 196–197 (fig. 200); Ris, Ann. Soc. Entomol. Belg. lv. 1911, pp. 244–245; Ris, Nova Guinea, xiii. Zool., Livr. 2, pp. 111–112.

21. *GYNACANTHA MACLACHLANI Krüger.

Gynacantha maclachlani Krüger, Stettin. Entomol. Zeitg. 1898, pp. 277–287, figs. p. 280 and p. 319; Martin, Cat. Coll. Selys, Æschn. pp. 200–201 (fig. 205).

22. *GYNACANTHA HYALINA Selys.

Acanthagyna hyalina Kirby, Cat. Odonata, p. 95.

Gynacantha hyalina Selys, Ann. Mus. Civ. Genova, 2. x. (xxx.) 1890, p. 50; Krüger, Stettin. Entomol. Zeitg. 1898, pp. 277–283; Martin, Cat. Coll. Selys, Æchn. pp. 198–199 (fig. 203).

23. ANAX GUTTATUS (Burm.).

Anax guttatus Kirby, Cat. Odonata, p. 84; Laidlaw, Proc. Zool. Soc. London, 1902, p. 78; Martin, Mission Pavie, Névroptères, (sep.) p. 14; Martin, Cat. Coll. Selys, Æschn. pp. 23–24 (fig. 17); Ris, Senckenberg Naturfors. Gesellsch. xxxiv. 1913, p. 527.

1 ♂, 1 ♀. Lio Matu, 2. xi. 14.

24. *ANACIÆSCHNA JASPIDEA (Burm.).

Anaciæschna jaspidea Kirby, Cat. Odonata, p. 86; Krüger, Stettin. Entomol. Zeitg. 1898, pp. 274–275; Martin, Cat. Coll. Selys, Æschn. pp. 30–31 (fig. 25).

GOMPHINÆ.

[For references to literature, *see* Laidlaw, Proc. Zool. Soc. London, 1914, pp. 51–63: "Contributions to a Study of the Dragonfly Fauna of Borneo.—Part II. The Gomphinæ and Chlorogomphinæ" (plate i.).]

25. ICTINUS ACUTUS Selys (MSS.).

26. *ICTINUS DECORATUS Selys.

27. ICTINUS MELÆNOPS Selys.

28. GOMPHIDIA MACLACHLANI Selys.

29. *GOMPHIDIA KARSCHI Selys.

30. SIEBOLDIUS JAPONICUS Selys.

31. *MACROGOMPHUS ALBARDÆ Selys.

32. MACROGOMPHUS DECEMLINEATUS Selys.

33. MACROGOMPHUS QUADRATUS Selys.

34. MICROGOMPHUS CHELIFER Selys.

35. *LEPTOGOMPHUS SEMPERI Selys.

36. LEPTOGOMPHUS WILLIAMSONI Laidlaw.

37. BURMAGOMPHUS VERMICULATUS Martin, subsp. *insularis* Laidlaw.

38. HETEROGOMPHUS ICTEROPS Martin, subsp. *borneensis* Laidlaw.

39. HETEROGOMPHUS SUMATRANUS Krüger.

Heterogomphus sumatranus Laidlaw, Proc. Zool. Soc. London, 1917, p. 232.

LIBELLULIDÆ.

CORDULIINÆ.

40. HEMICORDULIA ASSIMILIS Selys.

Hemicordulia (?) *assimilis* Kirby, Cat. Odonata, p. 46.
Hemicordulia assimilis Laidlaw, Proc. Zool. Soc. London, 1913, pp. 64–65; Martin, Cat. Coll. Selys, Cordul. pp. 11–12; Ris, Nova Guinea, ix. Zool. 3, pp. 501–502 (fig. 21).

41. AZUMA AUSTRALIS (Hagen).

Epophthalmia australis Kirby, Cat. Odonata, p. 54; Martin, Cat. Coll. Selys, Cordul. p. 63; Ris, Ann. Soc. Entomol. Belg. lv. 1911, pp. 248–250 (figs. 14, 15).

42. *AZUMA VITTIGERA (Ramb.).

Epophthalmia vittigera Kirby, Cat. Odonata, p. 54; Martin, Mission Pavie, Névroptères, (sep.) p. 8; id., Cat. Coll. Selys, Cordul. pp. 62–63.

43. MACROMIA CINCTA Ramb.

Macromia cincta Kirby, Cat. Odonata, p. 55; Krüger, Stettin. Entomol. Zeitg. 1899, p. 325; Martin, Cat. Coll. Selys, Cordul. p. 68; Laidlaw, Proc. Zool. Soc. London, 1913, p. 69.

2 ♂ ♂. Baram.

Length of abdomen 49 mm., of hinder-wing 45 mm.

44. *MACROMIA BORNEENSIS Krüger.

Macromia borneensis Krüger, Stettin. Entomol. Zeitg. 1899, pp. 330–332; Martin, Cat. Coll. Selys, Cordul. pp. 68–69.

45. *MACROMIA GERSTAECKERI Krüger.

Macromia gerstaeckeri Krüger, Stettin. Entomol. Zeitg. pp. 335–338; Laidlaw, Proc. Zool. Soc. London, 1902, pp. 76–78; Martin, Cat. Coll. Selys, Cordul. p. 70.

46. MACROMIA WESTWOODI Selys.

Macromia westwoodi Kirby, Cat. Odonata, p. 55; Krüger, Stettin. Entomol. Zeitg. 1899, pp. 325–326; Martin, Mission Pavie, Névroptères, (sep.) p. 8; Laidlaw, Proc. Zool. Soc. London, 1913, p. 69; Martin, Cat. Coll. Selys, Cordul. p. 72.

1 ♂. Lio Matu, 30. x. 14.

Length of abdomen 42 mm., of hinder-wing 41·5 mm.

47. MACROMIA EUTERPE Laidlaw.

Macromia euterpe Laidlaw, Proc. Zool. Soc. London, 1915, pp. 26–29, figs. 1, 2.

2 ♂ ♂, 1 ♀. Kinabalu. 1 ♂, 1 ♀. Mt. Merinjak, 600 ft., 24. v. 14.

48. *MACROMIA CINGULATA Ramb.

Macromia cingulata Kirby, Cat. Odonata, p. 55; Martin, Mission Pavie, Névroptères, (sep.) p. 8; Martin, Cat. Coll. Selys, Cordul. p. 70.

[Of the six Bornean species here recorded I have seen examples of three only. The large female specimen referred to in a previous paper (Proc. Zool. Soc. London, 1913, p. 68) is probably a female specimen of *Epophthalmia australis* Hagen.

Macromia euterpe Laidlaw appears to be closely allied to *M. westwoodi* Selys. Both species are characterized by having segments 1–6 of the abdomen of metallic-green lustre, whilst the remaining four segments are black, save for the yellow basal mark on 7.

On the other hand, the anal angle in the wings of the males are different in shape: that of *M. euterpe* as shown in the figure given (*loc. cit.* text-fig. 1, A) is rather deeply indented, that of *M. westwoodi* much more nearly straight. But the readiest means of discriminating the two species is afforded by the anal appendages of the male. In the specimens of *M. euterpe* I have examined, the upper pair are in every case almost destitute of an external tooth, and are but little shorter than the lower appendix.

In the case of *M. westwoodi* both the specimen before me and that described by de Selys have the external tooth well developed, and the lower appendage exceeds the upper pair in length very considerably, projecting beyond them by nearly a third of its total length when seen in profile.

For the rest I record *M. cingulata* Ramb. and *M. gerstaeckeri* on Martin's authority.]

49. MACROMIDIA FULVA Laidlaw.

Macromidia fulva Laidlaw, Proc. Zool. Soc. London, 1915 pp. 29, 30, text-fig. 3.

1 ♂. Kinabalu. 1 ♀. Mt. Matang, 4. xii. 13.

The male is the type of the species and is in the British Museum.

The female is very immature. The body-colour is a pale brown, with darker bands at bases of abdominal segments 3–7, and there is a brown basal spot on each wing extending nearly to ax_2, the rest of the wing being perfectly clear. Abd. 34 mm., h. w. 35 mm.

50. IDIONYX DOHRNI Krüger, subsp. BORNEENSIS.

Idionyx dohrni Krüger, subsp. *borneensis* Laidlaw, Proc. Zool. Soc. London, 1913, p. 67.

51. METAPHYA MICANS Laidlaw.

Metaphya micans Laidlaw, Sarawak Mus. Journ. No. 2, 1912, pp. 65–67, pl. i.; id., Proc. Zool. Soc. London, 1913, pp. 65–66 (pl. iv. figs. 1, 3).

The genus occurs in Borneo, New Guinea, and, I believe, in New Caledonia.

LIBELLULINÆ.

GROUP I. (of Ris).

52. TETRATHEMIS IRREGULARIS HYALINA Kirby.

Tetrathemis irregularis hyalina Ris, Cat. Coll. Selys, Libell. p. 47.

2 ♂ ♂. Matang Rd., 25. iii. 10. 1 ♂. Retuh, 16. v. 14. 1 ♂. Limbang, 8. ix. 09.

53. *TETRATHEMIS FLAVESCENS Kirby.

Tetrathemis flavescens Ris, Cat. Coll. Selys, Libell. p. 52.

1 ♂. Sarawak. Autotype in Brit. Mus. ♀ unknown.

54. ODA DOHRNI (Krüger).

Oda dohrni Ris, Cat. Coll. Selys, Libell. pp. 62–63 (figs. 25–28).

4 ♂ ♂, 3 ♀ ♀. Matang Rd.

55. HYLÆOTHEMIS CLEMENTIA Ris.

Hylæothemis clementia Ris, Cat. Coll. Selys, Libell. pp. 64–65 (figs. 29, 30); Laidlaw, Journ. Straits Branch R. As. Soc. No. 63, 1912, p. 95, pl., fig. 3.

1 ♀. Mt. Batu Lawi (allotype). Sarawak Museum.

GROUP II. (of Ris).

56. PORNOTHEMIS SERRATA Krüger.

Pornothemis serrata Ris, Cat. Coll. Selys, Libell. pp. 92, 93 (fig. 64).

5 ♂ ♂, 2 ♀ ♀. Matang Rd.

57. ORCHITHEMIS XANTHOSOMA Laidlaw.

Orchithemis xanthosoma Ris, Cat. Coll. Selys, Libell. pp. 1056–1057 (fig. 615).

3 ♂ ♂, 2 ♀ ♀. Matang Rd. Type ♂ in British Museum; allotype ♀, coll. Selys.

58. ORCHITHEMIS PULCHERRIMA Brauer.

Orchithemis pulcherrima Ris, Cat. Coll. Selys, Libell. pp. 85–86 (figs. 54, 55).

1 ♀. Sadong Hill. 1 ♂, 2 ♀ ♀. Matang Rd., 24. vi. 09. 3 ♂ ♂, 3 ♀ ♀. Baram (*C. Hose*).

59. *ORCHITHEMIS PRUINANS (Selys).

Orchithemis pruinans Ris, Cat. Coll. Selys, Libell. pp. 87–88 (figs. 56, 57).

60. LYRIOTHEMIS CLEIS Brauer.

Lyriothemis cleis Ris, Cat. Coll. Selys, Libell. pp. 108–111 (figs. 78, 79, 80).

1 ♂. Limbang. 2 ♂ ♂. Mt. Murud, xi–xii. 14. 1 ♀. Tatau. 1 ♂. Selindong, 12. vi–xi. (2 ♂ ♂, 1 ♀. Baram; *C. Hose.*)

61. *LYRIOTHEMIS BIAPPENDICULATA (Selys).

Lyriothemis biappendiculata Ris, Cat. Coll. Selys, Libell. pp. 106–107 (figs. 71, 76, 77).

62. NESOXENIA LINEATA (Selys).

Nesoxenia lineata Ris, Cat. Coll. Selys, Libell. pp. 126–128 (figs. 93, 94).

1 ♂. Matang Rd.

63. *LATHRECISTA ASIATICA (Fabr.).

Lathrecista asiatica asiatica Ris, Cat. Coll. Selys. Libell. pp. 130–132 (figs. 95, 96, 97).

64. AGRIONOPTERA INSIGNIS (Ramb.).

Agrionoptera insignis insignis Ris, Cat. Coll. Selys. Libell. pp. 137–138 (fig. 99).

1 ♂. Buntal, vi. 1910. *Thorax* dark metallic green, lighter markings almost lost. *Abdomen* with segments 3–8 scarlet-red, each with apical, black ring; on 8 about one sixth the length of segment. *Wings* suffused with golden yellow, especially at apices; basal marks golden brown; on fore-wing *sc* to *ax'*$_1$, *cu* to *Ac*. Hinder-wing *sc* not reaching *ax'*$_1$, *cu* to *Ac*.

Abd. 28 mm., h. w. 31 mm. Pt. 3 mm.

65. AGRIONOPTERA SEXLINEATA Selys.

Agrionoptera sexlineata Ris, Cat. Coll. Selys, Libell. pp. 144–145 (figs. 102, 103).

1 ♂, 1 ♀. Baram, 15. x. 1910.

The female from Baram has the wings hyaline throughout, and the red marking on the 7th abd. segment only.

66. CRATILLA METALLICA (Brauer).

Cratilla metallica Ris, Cat. Coll. Selys, Libell. pp. 152–153 (figs. 108, 109).

1 ♂. Mt. Murud, 5. xii. 14. 1 ♂, 1 ♀. Matang Rd., 13. x. 09.

67. CRATILLA LINEATA (Brauer).

Cratilla lineata Ris, Cat. Coll. Selys, Libell. pp. 153–155 (figs. 110, 111).

68. POTAMARCHA OBSCURA (Ramb.).

Potamarcha obscura Ris, Cat. Coll. Selys, Libell. pp. 156–157 (fig. 112).

69. ORTHETRUM GLAUCUM (Brauer).

Orthetrum glaucum Ris, Cat. Coll. Selys, Libell. pp. 233–234; Laidlaw, Proc. Zool. Soc. London, 1915, p. 25.

70. ORTHETRUM PRUINOSUM CLELIA (Selys).

Orthetrum pruinosum clelia Ris, Cat. Coll. Selys, Libell. pp. 242–243.

Orthetrum clelia Laidlaw, Proc. Zool. Soc. London, 1915, p. 26.

71. ORTHETRUM SABINA (Drury).

Orthetrum sabina Ris, Cat. Coll. Selys, Libell. pp. 223–225 (figs. 133, 149).

72. ORTHETRUM TESTACEUM (Burm.).

Orthetrum testaceum testaceum Ris, Cat. Coll. Selys, Libell. pp. 234–236; Laidlaw, Proc. Zool. Soc. London, 1915, p. 26.

73. ORTHETRUM CHRYSIS (Selys).

Orthetrum chrysis Ris, Cat. Coll. Selys, Libell. p. 237.

GROUP IV. (of Ris).

74. NANNOPHYA PYGMÆA Ramb.

Nannophya pygmæa Ris, Cat. Coll. Selys, Libell. pp. 347–348 (figs. 196, 197).

6 ♂♂, 2 ♀♀. Sarawak.

75. BRACHYGONIA OCULATA (Brauer).

Brachygonia oculata Ris, Cat. Coll. Selys, Libell. pp. 353–354 (figs. 203, 204).

3 ♂♂. 4th Mile, Rock Rd., Sarawak, 1909.

76. BRACHYGONIA OPHELIA Ris.

Brachygonia ophelia Ris, Cat. Coll. Selys, Libell. p. 354 (fig. 205).

1 ♀. 4th Mile, Rock Rd., Sarawak, 1910.

77. TYRIOBAPTA TORRIDA Kirby.

Tyriobapta torrida Ris, Cat. Coll. Selys, Libell. pp. 355–356 (figs. 206, 208), and pp. 1120–1121 (fig. 643).

1 ♀. Sadong. 1 ♀. Matang Rd., vi. 09.

78. TYRIOBAPTA LAIDLAWI Ris.

Tyriobapta laidlawi Ris, Cat. Coll. Selys, Libell. pp. 1121–1122 (fig. 644).

1 ♂. Sarawak (autotype). Coll. Ris.

79. TYRIOBAPTA KUKENTHALI (Karsch).

Tyriobapta kukenthali Ris, Cat. Coll. Selys, Libell. pp. 357–358 (fig. 209), and p. 1122.

3 ♂♂. Sarawak.

80. BRACHYDIPLAX CHALYBEA CHALYBEA Brauer.

Brachydiplax chalybea Ris, Cat. Coll. Selys, Libell. p. 363.
Brachydiplax chalybea chalybea id. op. cit. p. 1123.

1 ♂. Santubang, 19. i. 10. 1 ♂. Baram (*C. Hose*). 1 ♂. Kotabelud, 17. viii. 13.

81. Raphisma inermis Ris.

Raphisma inermis Ris, Cat. Coll. Selys, Libell. pp. 370–371 (fig. 222).

3 ♂ ♂. Sarawak.

Group VI. (of Ris).

82. *Diplacodes trivialis (Ramb.).

Diplacodes trivialis Ris. Cat. Coll. Selys, Libell. pp. 468–470 (figs. 293, 294).

83. *Crocothemis servilia (Drury).

Crocothemis servilia Ris, Cat. Coll. Selys, Libell. pp. 539–542 (fig. 320).

84. *Neurothemis disparilis Kirby.

Neurothemis disparilis Ris, Cat. Coll. Selys, Libell. p. 566.

85. Neurothemis fluctuans Fabr.

Neurothemis fluctuans Ris, Cat. Coll. Selys, Libell. pp. 566–569.

1 ♂. 4th Mile, Rock Rd., Sarawak. 1 ♂, 1 ♀. Limbang, 20. vi. 11. 1 ♀. N. Merinjak. 13. xi. 14. 1 ♂, 1 ♀. Baram (*C. Hose*).

86. Neurothemis terminata Ris.

Neurothemis terminata Ris, Cat. Coll. Selys, Libell. pp. 569–572 (figs. 328, 329, 334, 335).

2 ♂ ♂. Matang Rd. 1 ♂. Matang Mountain. 1 ♂. Bidi, viii. 98. 1 ♂. Buntal, 16. iii. 12. 1 ♂. Samarakan, 17. vi. 10.

87. Rhodothemis rufa (Ramb.).

Rhodothemis rufa Ris, Cat. Coll. Selys, Libell. pp. 592, 593 (fig. 350).

1 ♀. Retuh. 16. v. 14.

Group VII. (of Ris).

88. Pseudagrionoptera diotima Ris.

Pseudagrionoptera diotima Ris, Cat. Coll. Selys, Libell. pp. 748 749 (figs. 425, 426).

1 ♀. Sarawak.

89. Trithemis aurora (Burm.).

Trithemis aurora Ris, Cat. Coll. Selys, Libell. pp. 775–778 (fig. 442); Laidlaw, Proc. Zool. Soc. London, 1915, p. 26.

1 ♂, 1 ♀. Kinabalu. 2 ♂ ♂. Ulu Akar, 14. xi. 14. ♂. Mt. Murud, 18. vii. 14. 1 ♂. Samarakan, 17. vi. 10.

90. TRITHEMIS FESTIVA (Ramb.).

Trithemis festiva Ris, Cat. Coll. Selys, Libell. pp. 796–799 (figs. 456, 457); Laidlaw, Proc. Zool. Soc. London, 1915, p. 26.

3 ♂ ♂. Kinabalu. 1 ♀. Mt. Merinjak.

91. ZYGONYX IRIS Selys.

Zygonyx iris Ris, Cat. Selys, Libell. pp. 820–823 (fig. 478); Laidlaw, Proc. Zool. Soc. London, 1915, p. 26.

2 ♂ ♂. Kinabalu. 1 ♀. Mt. Murud, 2. xii. 14.

92. ONYCHOTHEMIS CULMINICOLA CELEBENSIS Ris.

Onychothemis culminicola Förster, subsp. *celebensis* Ris, Cat. Coll. Selys, Libell. pp. 835–836.

1 ♂. Tatau.

Under lip brown, upper lip and face brown, with faint metallic blue reflexion; thorax brown, also with rather a metallic tinge. Abdomen entirely scarlet; anal appendages—upper pair red at base, distal two-thirds black; lower appendage red, terminating in a pair of fine black points. Wings lightly suffused with yellow. Legs black. Abd. 32 mm.; h. w. 35 mm. Scarcely fully mature.

93. *ONYCHOTHEMIS CULMINICOLA CULMINICOLA Förster.

Onychothemis culminicola culminicola Ris, Cat. Coll. Selys, Libell. pp. 835, 836.

GROUP X. (of Ris).

94. HYDROBASILENS CROCEUS (Brauer).

Hydrobasilens croceus Ris, Cat. Coll. Selys, Libell. pp. 969–970 (fig. 562).

95. TRAMEA LIMBATA (Desjardins).

Tramea limbata Kirby, Cat. Odonata, p. 4.

Tramea translucida Kirby, loc. cit. p. 3.

Tramea limbata Ris, Cat. Coll. Selys, Libell. pp. 979–988 (figs. 563, 568, 569).

96. RHYOTHEMIS PHYLLIS PHYLLIS (Sulzer).

Rhyothemis phyllis phyllis Ris, Cat. Coll. Selys, Libell. pp. 939–940 (fig. 540, pl. v.).

97. *RHYOTHEMIS ATERRIMA Selys.

Rhyothemis aterrima Ris, Cat. Coll. Selys, Libell. p. 953.

98. RHYOTHEMIS PYGMÆA (Brauer).

Rhyothemis pygmæa Ris, Cat. Coll. Selys, Libell. p. 955.

99. RHYOTHEMIS OBSOLESCENS Kirby.

Rhyothemis obsolescens Ris, Cat. Coll. Selys, Libell. pp. 958-959 (pl. vii.).

100. RHYOTHEMIS TRIANGULARIS Kirby.

Rhyothemis triangularis Ris, Cat. Coll. Selys, Libell. pp. 962-963.

101. *ZYXOMMA PETIOLATUM Ramb.

Zyxomma petiolatum Ris, Cat. Coll. Selys, Libell. pp. 903-905 (fig. 523).

102. *THOLYMIS TILLARGA (Fabr.).

Tholymis tillarga Ris, Cat. Coll. Selys, Libell. pp. 913-915 (figs. 531, 532).

103. PANTALA FLAVESCENS (Fabr.).

Pantala flavescens Ris, Cat. Coll. Selys, Libell. pp. 917-920 (fig. 533).

104. *CAMACINIA HARTERTI Karsch.

Camacinia harterti Ris, Cat. Coll. Selys, Libell. pp. 928-929 (figs. 538, 539).

105. UROTHEMIS SIGNATA INSIGNATA (Selys).

Urothemis signata insignata Ris, Cat. Coll. Selys, Libell. pp. 1024-1025.

106. *ÆTHRIAMANTA GRACILIS (Brauer).

Brachydiplax gracilis Kirby, Cat. Odonata, p. 22.
Brachydiplax melænops Kirby, loc. cit.
Æthriamanta gracilis Ris, Cat. Coll. Selys, Libell. pp. 1032-1033 (figs. 597, 598).

ZYGOPTERA.

CALOPTERYGINÆ.

107. NEUROBASIS CHINENSIS (Linn.).

Neurobasis chinensis Kirby, Cat. Odonata, p. 102; Förster, Ann Soc. Entomol. Belg. xli. 1897, pp. 204-210; Krüger, Stettin. Entomol. Zeitg. 1898, pp. 74-75; Laidlaw, Proc. Zool. Soc. London, 1902, pp. 86-87.
Neurobasis chinensis chinensis Ris, Tijd. v. Entomol. lviii. 1915, p. 6.

108. MATRONOIDES CYANEIPENNIS Förster.

Matronoides cyaneipennis Förster, Wiener Entomol. Zeitg 1897, iii.; id., Ann. Soc. Entomol. Belg. xl. 1897. (sep.) pp. 1–5 Laidlaw. Journ. Straits Branch R. Asiat. Soc. [63] 1912, p. 95 id., Proc. Zool. Soc. London, 1915, p. 30.

6 ♂ ♂. Mt. Selinguid and Mt. Batu Lawi, 3500 ft., 30. v. 11. 14 ♂ ♂, 5 ♀ ♀. Mt. Kinabalu. ix. 1913, up to 3000 ft.

109. VESTALIS AMŒNA Selys.

Vestalis amœna Kirby, Cat. Odonata, p. 103; Krüger, Stettin. Entomol. Zeitg. 1898, p. 75: Laidlaw, Proc. Zool. Soc. London, 1902, p. 87; id., Proc. Zool. Soc. London, 1915, pp. 30–31.

11 ♂ ♂, 5 ♀ ♀. Mt. Kinabalu up to 3000 ft.

110. VESTALIS BERYLLÆ Laidlaw.

Vestalis beryllæ Laidlaw, Sarawak Mus. Journ. ii. 6. 1915, p. 273.

1 ♂ (autotype). Retuh. Specimen in Brit. Mus.

Wings hyaline, slightly tinged with yellow. A single row of cells between Cu$_1$ and Cu$_2$. Body metallic green. Legs black. The species is remarkable for the great relative length of the abdomen (70 mm.) as against 40 mm. for the hinder-wing.

EPALLAGINÆ.

111. PSEUDOPHÆA TRICOLOR (Selys).

Pseudophæa tricolor Kirby, Cat. Odonata, p. 109.

8 ♂ ♂. Retuh, 14. ix. 14. 2 ♂ ♂, 2 ♀ ♀. Saribas (3 ♂ ♂, Baram; *C. Hose*).

112. PSEUDOPHÆA SUBCOSTALIS (Selys).

Pseudophæa subcostalis Kirby, Cat. Odonata, p. 109; Laidlaw, Proc. Zool. Soc. London, 1915, pp. 32–33.

4 ♂ ♂. Tampassuk, 19. viii. 13. 2 ♂ ♂. Saribas. 3 ♂ ♂. Mt. Murud. 4 ♂ ♂. Ulu Akar.

113. PSEUDOPHÆA SUBNODALIS Laidlaw.

Pseudophæa subnodalis Laidlaw, Proc. Zool. Soc. London, 1915, p. 31.

13 ♂ ♂, 1 ♀?. Mt. Kinabalu, ix. 13.

114. PSEUDOPHÆA BASALIS Laidlaw.

Pseudophæa basalis Laidlaw, Proc. Zool. Soc. London, 1915, p. 32.

4 ♂ ♂. Kinabalu, 11–18. ix. 13.

The males of these four species are at first sight very much alike. They may be discriminated as follows :—

A. Opaque colouring of hinder-wing begins at nodus or one or two cells before. Its margin runs transversely across the wing; never a dark subcostal band extending to the wing-base.
Abd. 35 + 1 mm., h. w. 27·5 mm. *P. tricolor* Selys.

B. Opaque colouring of hinder-wing begins about half-way between wing-base and nodus. Its margin runs obliquely outwards and backwards, and is rather irregular : usually a hyaline indentation about 4–6 cells deep between M_1 and Cu_1. Dark band in subcostal space of all four wings extending to wing-base in adult specimens, reaching the nodus in the fore-wing. Apex of fore-wing tipped with dark brown from the middle of the pterostigma.
Abd. 30 + 1 mm., h. w. 25 mm. *P. subcostalis* Selys.

C. Opaque area of hinder-wing begins at about two-thirds of the distance from the wing-base to the nodus, but *area between* M_{1+2} *and* R *is always hyaline up to nodus.* Dark subcostal stripe not so well marked as in *P. subcostalis*, and scarcely indicated on the fore-wing, which also has much less opacity at its apex.
Abd. 35 + 1 mm., h. w. 28–30 mm. *P. subnodalis* Laidlaw.

D. Hinder-wing opaque from the base to apex except for the basal space, and for certain quite irregular areas which in some specimens occur on the wings. Costal and subcostal spaces of fore-wing dark brown up to nodus
Abd. 35 + 1 mm., h. w. 27–28 mm. *P. basalis* Laidlaw.

Unfortunately I do not know the females.

These species probably all belong to the group *P. variegata* (Ramb.). The group occurs in all parts of the Sondaic area.

115. PSEUDOPHLÆA IMPAR INÆQUIPAR (Selys).

Pseudophæa inæquipar Kirby, Cat. Odonata, p. 109.

4 ♂ ♂. Tatau.

At most these are but a local race of the older species *P. impar* (Selys) from Malacca and Sumatra.

Its nearest allies seem to be *P. dispar* (Ramb.) and *P. fraseri* Laidlaw from W. India, though the relationship is not very close.

116. DYSPHÆA LUGENS Selys.

Dysphæa lugens Kirby, Cat. Odonata, p. 110.

2 ♂ ♂. Limbang River, iv. 10. 1 ♀ (?). Retuh, 16. v. 14.

The wings of the female specimen show in light hyaline brown a colour-pattern identical with that of the male.

♂. Abd. 38 mm. + 1·5 mm., h. w. 32 mm. ♀. Abd. 30 mm., h. w. 29 mm.

117. DYSPHÆA LIMBATA Selys.

Dysphaea limbata Kirby, Cat. Odonata, p. 40.

3 ♂ ♂. Tatau. 1 ♂. Baram (*C. Hose coll.*; no date).

The male from Baram belongs to the race *semilimbata* of Selys. It is without the black costal line between the nodus and pterostigma of the fore-wing. All the specimens have the hyaline parts of the wings suffused with yellow-brown.

♂. (Baram). Abd. 34 mm.+1·5 mm., h. w. 30 mm.

♂. Tatau. Abd. 35 mm.+1·5 mm., h.w. 30·5 mm.

LIBELLAGINÆ.

118. RHINOCYPHA BISERIATA Selys.

Rhinocypha biseriata Kirby, Cat. Odonata, p. 113.

Very closely related to *R. angusta* Selys from Sumatra and to *R. perforata* Perch. from Malacca and Lower Siam. The group is Indo-Chinese and Sondaic in distribution.

119. RHINOCYPHA KARSCHI Krüger.

Rhinocypha karschi Krüger, Stettin. Entomol. Zeitg. 1898, pp. 83–85; Laidlaw, Proc. Zool. Soc. London, 1902, p. 90.

4 ♂ ♂. Limbang, ix. 09.

The species stands alone, without, so far as I know, near allies. It is confined to the Sondaic area.

120. *RHINOCYPHA STYGIA Förster.

Rhinocypha stygia Förster, Ann. Soc. Entomol. Belg. xli. 1897, pp. 210–211.

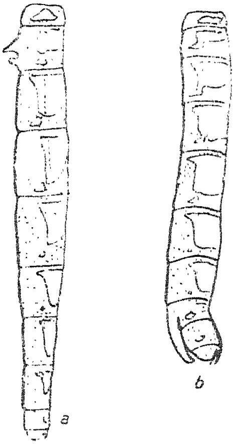
121. RHINOCYPHA MOULTONI Laidlaw. (Text-fig. 1, *a*, *b*.)

Rhinocypha moultoni Laidlaw, Proc. Zool. Soc. London, 1915, p. 35.

4 ♂ ♂, 6 ♀ ♀. Kinabalu, Sept. 1913.

The adult female of this species resembles that of *R. stygia* Förster very closely, to judge at least by Förster's rather brief description. But the fully adult male is so brightly coloured about the body—much more so than the female—that I do not think it possible that *stygia*, which is entirely black about the body, can be merely a very adult specimen of the same species. The four males of *moultoni* that I have been able to examine are fully mature, and it is interesting to find that they retain on the abdomen the colour-pattern characteristic of the teneral female, which is lost in the mature female. For whereas the male retains the paired dorsal spots of the abdomen from segment 2 to 9 as rich orange-red marks in addition to the yellow paired lateral marks, these dorsal marks are entirely lost in the fully adult female, but are very conspicuous in newly-emerged females as large lemon-yellow areas covering about three-quarters of the dorsum of each segment from 2 to 8: fused at their bases with the lateral system. (In the male the two series, dorsal and lateral, are fused for their whole length from 2 to 6.) So that,

Text-figure 1, *a*, *b*.



Lateral view of colour-pattern of abdomen of *Rhinocypha moultoni*.
a, male; *b*, immature female.

whilst not refusing to admit the possibility of *R. stygia* being the extremely adult stage of *R. moultoni*, I do not think it at all likely, and retain here the latter species as distinct.

122. Rhinocypha cucullata Selys.

Rhinocypha cucullata Kirby, Cat. Odonata, p. 114.

6 ♂ ♂. Tatau. 5 ♂ ♂. Saribas.

An isolated species, confined apparently to Borneo.

123. *Rhinocypha humeralis Selys.

Rhinocypha humeralis Kirby, Cat. Odonata, p. 114.

124. *Rhinocypha eximia Selys.

Rhinocypha eximia Kirby, Cat. Odonata, p. 114.

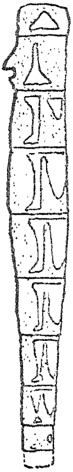
125. Rhinocypha sp. A.

This species was identified for me by Martin. He has named and described it in the forthcoming monograph of the Calopterygidæ in the Selysian collection, the appearance of which has been very considerably delayed. As I do not wish to forestall him, I note here only that the species appears to me to be related to Förster's *R. aurulenteus* from Buru, and perhaps more remotely to *R. cucullata* Selys. I have examined a series of specimens (♂) from Lio Matu and Tatau.

126. RHINOCYPHA sp. B. (Text-fig. 2.)

The remarks made on the previous species refer also to the present one, which appears to be allied to *R. moultoni*. I have seen 5 specimens from Mt. Batu Lawi, all males.

Text-figure 2.



Lateral view of colour-pattern of abdomen of *Rhinocypha* sp. B.

[The primitive marking of the abdomen of the genus *Rhinocypha*, and perhaps of *Micromerus*, is probably a series of paired dorsal marks, and outside these on either side a series of lateral markings, the latter originally possibly a line extending along the length of the segment, but now in many cases broken up into anterior and posterior spots.

The species which in this paper I refer to as *Rhinocypha* sp. A seems to preserve the primitive colouring to a fairly typical extent; this is also the case in *R. moultoni* and in *Rhinocypha* sp. B. Other species show various modifications of the colour-pattern, which, it may be noted, may be either blue, orange, red, or yellow. Thus, in *R. cucullata* for example, in the males only the lateral colour-marks are retained, save on segments 8 to 9, which have also dorsal markings. In *R. aurulentus* Förster from Buru only the lateral marks are retained; whilst in the exquisite *R. iridea* Selys from Burma only marks belonging to the dorsal series are to be seen. Lastly, in some presumably specialized forms—*e. g.*, *R. stygia* Förster—these markings have disappeared altogether.]

Diagnostic table for males of Bornean species of Rhinocypha.

A. All four wings with opaque areas.	
a. Opaque area of hinder-wing with hyaline windows, "mesothoracic triangle" present	*R. biseriata* Selys.
b. Opaque area of wings without hyaline windows.	
1. Large antehumeral blue ray on thorax.	
α. Terminal two-fifths of wings opaque	*R. humeralis* Selys.
β. Terminal fourth of wings opaque	*R. eximia* Selys.
2. Antehumeral band of synthorax narrow.	
γ. Terminal opaque area of wings beginning at level of prostigma in front; posterior tibiæ not dilated; slight enlargement of posterior margin of second abdominal segment	*Rhinocypha* sp. A.
δ. Terminal two-fifths of wings opaque. Posterior tibiæ dilated, blue on anterior surface. Marked enlargement of posterior margin of second abdominal segment	*R. cucullata* Selys.
B. Hinder-wings only with opaque markings. Dorsal marks of abd. segments 2–8 *red*	*R. karschi* Krüger.
C. No opaque markings on wings.	
1. Abdominal markings lost	*R. stygia* Förster.
2. Dorsal markings on abdomen red, lateral markings yellow.	
a. Apex of clypeus marked with orange-yellow. Lateral abdominal markings from segment 2–5 broken into an anterior line and posterior spot. The anterior line is entirely fused with the dorsal mark on these segments. From 6–8 the lateral series is represented only by an anterior spot fused to the dorsal marks	*R. moultoni* Laidlaw.
β. Apex of clypeus black. Lateral abdominal markings present as a complete band of rather irregular outline on segments 2–7, only fused with the dorsal marks at its extreme base, and not at all on segments 2–3, on which segments the dorsal mark is small or absent	*Rhinocypha* sp. B.

127. Rhinoneura villosipes Laidlaw.

Rhinoneura villosipes Laidlaw, Proc. Zool. Soc. London, 1915, pp. 33–35 (text-figs. 4, 5 A).

1 ♂. Mt. Kinabalu.

Autotype in British Museum.

128. Micromerus aurantiacus Selys.

Micromerus aurantiacus Kirby, Cat. Odonata, p. 115.

2 ♂ ♂. Limbang.

129. Micromerus semiopacus Selys.

Micromerus semiopacus Kirby, Cat. Odonata, p. 115; Ris, Ann. Soc. Entomol. Belg. lv. 1911, pp. 233–234 (fig. 1).

3 ♂ ♂. Lio Matu. 2 ♂ ♂. Ulu Akar, xi. 14. 2 ♀ ♀. Lio Matu.

130. MICROMERUS HYALINUS Selys.

Micromerus hyalinus Kirby, Cat. Odonata, p. 115.

2 ♂ ♂. Baram, x. 1910. 2 ♂ ♂. Tatau. 3 ♂ ♂ ad., 3 ♂ ♂ juv., 3 ♀ ♀. Saribas.

131. MICROMERUS STICTICUS Selys.

Micromerus sticticus Kirby, Cat. Odonata, p. 115.

3 ♂ ♂. Tatau.

Incertæ sedis.

132. DEVADATTA ARGYROIDES (Selys).

Devadatta argyroides Kirby, Cat. Odonata, p. 111.

This genus seems to me to be not very remote in venation from the "Legion" *Megapodagrion*.

Legion MEGAPODAGRION.

133. *PODOLESTES ORIENTALIS Selys.

Podolestes orientalis Kirby, Cat. Odonata, p. 126; Krüger, Stettin. Entomol. Zeitg. 1898, pp. 98, 99.

134. PODOLESTES CHRYSOPUS Selys.

Podolestes chrysopus Kirby, Cat. Odonata, p. 126.

1 ♂, 1 ♀ in cop. Matang Rd., 28. x. 09. 2 ♂ ♂. Baram, vii. 09. 2 ♂ ♂. 4th Mile, Rock Rd., Sarawak, 24. vi. 09. 1 ♀. Matang Rd., 24. vi. 09.

135. RHINAGRION BORNEENSE (Selys).

Amphilestes borneensis Kirby, Cat. Odonata, p. 126; Karsch, Entomol. Nachr. xvii. (1891), no. 16, p. 2; Krüger, Stettin. Entomol. Zeitg. 1898, pp. 137–138.

10 ♂ ♂, 2 ♀ ♀. Lio Matu, 4. xi. 14. 1 ♀. Kuching, 5. xi. 09.

♂. Agrees fairly closely with the description of the type. The yellow mark on the dorsum of the thorax is triangular rather than oval, its base running quite transversely across the thorax, and its inner side close to the mid-dorsal carina. In one specimen, however, the anterior margin of the triangle is distinctly oblique, so that the mark becomes more nearly oval. The colouring of the ventral side of the thorax seems to vary with age; it is black in the fully adult specimens, but on the younger it is yellow with a smoky tinge.

Abdomen: segments 1–7 reddish brown, 1 with yellowish mark on dorsum, 2–7 with black apical ring, and 2 with pale subapical mark as well; 8, 9 white, enamelled; 8 with a reddish tinge of rather blue-white; 10 black.

Abd. 30 mm. + 1 mm., h. w. 21 mm.

♀. Head black, but with yellow median mark on post-clypeus and yellow margins around the eyes. Prothorax light golden brown above, paler below, with the posterior lobe whitish green. Thorax golden brown above, passing to grey-white below. Triangular marks on the dorsum as in the male.

Abdomen: segment 1 greenish white above, pale below; segments 2–7 reddish brown, progressively darker backwards, with subterminal grey-green rings; segments 8–10 black, 8 with lateral longitudinal whitish band.

Abd 27 mm., h. w. 25 mm.

(For generic name, see Calvert, Proc. Acad. Nat. Sci. Philadelphia, 1913, p. 258.)

136. *RHINAGRION ELOPURÆ (Selys).

Amphilestes elopuræ Kirby, Cat. Odonata, p. 126.

Legion PLATYCNEMIS.

137. CŒLICCIA OCTOGESIMA (Selys).

Cœliccia octogesima Kirby, Cat. Odonata, p. 128.

1 ♀. Matang Rd., 3. i. 10 (damaged).

138. CŒLICCIA MEMBRANIPES (Ramb.) (race NEMORICOLA Laidlaw?).

Cœliccia nemoricola Laidlaw, Journ. Straits Branch R. Asiat. Soc. [63] p. 95; id., Proc. Zool. Soc. London, 1915, p. 37.

Cœliccia membranipes race *nemoricola* Laidlaw, Proc. Zool. Soc. London, 1917, pp. 230–231.

Common on Mt. Kinabalu.

139. CŒLICCIA FLAVOSTRIATA Laidlaw.

Cœliccia flavostriata Laidlaw, Proc. Zool. Soc. London, 1917, pp. 223–224 (figs. 1, 2).

2 ♂♂. Mt. Merinjak, 21. v. 14. 1 ♂. Mt. Matang, 4. xii. 13.

Autotype in British Museum. Paratype in Coll. Mus. Sarawak and in my own collection.

140. CŒLICCIA CAMPIONI Laidlaw.

Cœliccia campioni Laidlaw, Proc. Zool. Soc. London, 1917, pp. 224–225 (figs. 3, 4).

1 ♂. Lio Matu, 31. x. 14.

141. CŒLICCIA MACROSTIGMA Laidlaw.

Cœliccia macrostigma Laidlaw, Proc. Zool. Soc. London, 1917, pp. 225–227 (figs. 5, 6).

1 ♂. Baram, 20. x. 10 (1 ♀?. 19. x. 10).

142. CŒLICCIA NIGROHAMATA Laidlaw.

Cœliccia nigrohamata Laidlaw, Proc. Zool. Soc. London, 1917, p. 228 (figs. 7, 8).

[CŒLICCIA BORNEENSIS (Selys).]

Cœliccia borneensis Kirby, Cat. Odonata, p. 128.

(See under *C. octogesima* (Selys), Laidlaw, Proc. Zool. Soc. London, 1917, p. 231.)

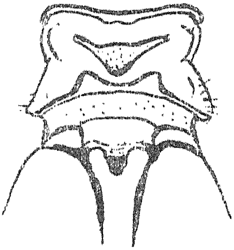
143. COPERA ATOMARIA (Selys). (Text-fig. 3.)

Copera atomaria Kirby, Cat. Odonata, p. 129.

(See also Krüger, Stettin. Entomol. Zeitg. 1898, pp. 103–107 : Ris, Tijdschr. v. Entomol. lviii. 1915, p. 7, sep.)

Upper anal appendages of male about one-half length of lower pair. Tibiæ not dilated. In the adult male the thorax is bronze-black above, with a few irregular yellow spots representing the antehumeral band. The sides of the thorax are mottled black and yellow, the legs are entirely red-brown. Abdomen black, with yellow lateral markings on segments 1 and 2 and a basal bluish-white ring on segments 3–6. Segment 10 and upper pair of anal appendages white, lower pair of appendages black; distal half marked with white dorsally.

Text-figure 3.



Prothorax of *Copera atomaria* seen from above.

Adult female coloured much as the male, but duller. The posterior femora have a row of black dots along their dorsal surface. The posterior thoracic margin of the female carries a pair of small triangular projections directed upwards and forwards. These are much less acute than the corresponding structures of the Sumatran species, *C. acutimargo* Krüger.

♂. Abd. 28 + 0·75 mm., h. w. 17·5 mm. ♀. Abd. 30 mm., h. w. 19 mm.

Specimens from Lio Matu seem to have been taken in company with *Caconeura verticalis* Selys; at least in many cases I found examples of both species papered together.

To what extent these Bornean specimens are to be regarded as distinct from other allied forms of the genus it is at present impossible to say. But I think it likely that a number of forms of the *vittata* series of the genus will ultimately be characterized. As I have seen only examples of one form from Borneo, I have retained for it the Selysian name.

Legion AGRION.

144. ONYCHARGIA ATROCYANA Selys.

Onychargia atrocyana Kirby, Cat. Odonata, p. 139; Krüger, Stettin. Entomol. Zeitg. 1898, p. 118; Ris, Nova Guinea, xiii. Zool. 2, pp. 94-95 (fig. 13).

1 ♂. Mt. Murud, 18. xii. 14. Very adult, lacking the last four abdominal segments.

145. CERIAGRION CERINORUBELLUM (Brauer).

Ceriagrion cerinorubellum Kirby, Cat. Odonata, p. 154; Krüger, Stettin. Entomol. Zeitg. 1898, pp. 119-120; Ris, Abh. d. Senckenberg Naturfors. Gesellsch. xxxiv. p. 519; id., Tijdschr. v. Entomol. lviii. 1915, p. 13 (sep.): Laidlaw, Rec. Indian Mus. xvi. part ii. p. 188.

2 ♂ ♂. 4th Mile, Rock Rd., Sarawak, 30. xi. 09. 3 ♂ ♂. Retuh, 16. v. 14.

146. CERIAGRION BELLONA Laidlaw.

Ceriagrion bellona Laidlaw, Sarawak Mus. Journal, ii. 1916, p. 274.

2 ♂ ♂. Mt. Matang, xii. 13. 1 ♂. Kinabalu, ix. 13.

Ab commences before the level of Ac. Wings in adult lightly tinged with yellowish brown. Excision on hind-margin of tenth abdominal segment Λ-shaped. Lower anal appendages (of male) about twice as long as upper pair. Head orange-brown above, greenish white below. Prothorax and synthorax coppery brown above, yellowish green below. Abdomen: first segment coppery brown, second to sixth carmine, seventh to tenth dull brown.

Abd. 28·5 mm., h. w. 20 mm.

147. PSEUDAGRION MICROCEPHALUM (Ramb.).

Pseudagrion microcephalum Kirby, Cat. Odonata, p. 153; Ris, Supplement Entomol. no. 5, 1916, pp. 40-43 (figs. 13-19); Laidlaw, Rec. Ind. Mus. xii. pp. 23-24 (fig. 1); Ris, Ann. Soc. Entomol. Belg. 1911, p. 235.

1 ♀ (damaged). 4th Mile, Rock Rd., Sarawak.

Dr. Ris gives a full synonymy of this species, and a description of several races characterized by the shape of the anal appendage of the male (Ris, Suppl. Entomol. *loc. cit.*).

The Bornean species seem to be below the average in size.

148. PSEUDAGRION PRUINOSUM (Burm.).

Pseudagrion pruinosum Kirby, Cat. Odonata, p. 153; Krüger, Stettin. Entomol. Zeitg. 1898, p. 119; Laidlaw, Sarawak Mus. Journal, ii. 1916, p. 275; Ris, Nova Guinea, xiii. Zool. 2, pp. 97-98 (fig. 18).

149. ACIAGRION BORNEENSE Ris.

Aciagrion borneense Ris, Ann. Soc. Entomol. Belg. 1911, pp. 234–235 (figs. 2–3).

1 ♀. Tabekang, 12. v. 14.

Occurs also in the Malay Peninsula.

150. AGRIOCNEMIS FEMINA (Brauer).

Agriocnemis femina Ris, Supplement Entomol. no. 5, 1916, pp. 22–26 (figs. 13, 17).

(For full synonymy of this species, see Ris, *loc. cit.*)

151. ARGIOCNEMIS RUBESCENS Selys.

Argiocnemis rubescens Kirby, Cat. Odonata, p. 158; Ris, Abh. d. Senckenberg Naturfors. Gesellsch. xxxiv. pp. 516–518.

(For this species also, consult Ris's paper quoted here.)

1 ♂. Malimau, 5. xi. 10. 1 ♂. Mt. Merinjak, 18. v. 14. 1 ♂. 4th Mile, Rock Rd., Sarawak.

152. AMPHICNEMIS WALLACEI Selys.

Amphicnemis wallacei Kirby, Cat. Odonata, p. 157; Ris, Ann. Soc. Entomol. Belg. lv. 1911, pp. 236–237 (figs. 4, 5); Laidlaw, Proc. Zool. Soc. London, 1913, p. 70.

1 ♂. Baram.

153. AMPHICNEMIS LOUISÆ Laidlaw.

Amphicnemis louisæ Laidlaw, Proc. Zool. Soc. London, 1913, p. 71, pl. iv. figs. 5, 5*a*; Ris, Tijdschr. v. Entomol. lviii. 1915, pp. 13–14.

154. AMPHICNEMIS REMIGER Laidlaw.

Amphicnemis remiger Laidlaw, Journal Straits Branch R. Asiat. Soc. [63] 1912, pp. 96–97, pl. fig. 4; id., Proc. Zool. Soc. London, 1913, p. 72.

1 ♂. Batu Lawi. 2 ♂ ♂ (imperfect). Murud, 20. xii. 14.

155. AMPHICNEMIS MADELENÆ Laidlaw.

Amphicnemis madelenæ Laidlaw, Proc. Zool. Soc. London, 1913, pp. 71–72 (pl. iv. figs. 6, 6*a*).

2 ♂ ♂. Kuching.

156. AMPHICNEMIS MARTINI Ris.

Amphicnemis martini Ris, Ann. Soc. Entomol. Belg. lv. 1911, pp. 237–238 (fig. 6); Laidlaw, Proc. Zool. Soc. London, 1913, pp. 72–73.

1 ♂. Limbang. 1 ♂. Mt. Merinjak, 22. xi. 14 (both imperfect).

And, in addition, I have before me 6 ♀ ♀ from Murud, 20. xi. 14, and 1 ♀ from Limbang which I have not identified with certainty; also a damaged female specimen from Tatau which is possibly identical with *A. gracilis* Krüger from Sumatra; and, lastly, 1 ♀ from Baram belonging to a different, and undetermined, species.

I hope to pay more attention to this interesting genus when opportunity offers.

157. PERICNEMIS STICTICA Selys.

Pericnemis stictica Kirby, Cat. Odonata, p. 158; Krüger, Stettin. Entomol. Zeitg. 1898, p. 158; Laidlaw, Proc. Zool. Soc. London, 1902, p. 386.

1 ♂. Limbang (in fragments).

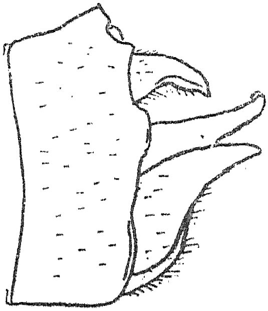
158. TEINOBASIS KIRBYI Laidlaw (?). (Text-fig. 4.)

Teinobasis kirbyi Laidlaw, Proc. Zool. Soc. London, 1902, pp. 386–387.

Teinobasis superba Laidlaw (nec Selys), Proc. Zool. Soc. London, 1917, p. 231.

1 ♂. Lio Matu, 4. xi. 14. (Specimen to be sent to British Museum.)

Text-figure 4.



Lateral view of anal appendages of *Teinobasis kirbyi*, ♂ (?).

M_2 and Ms united from their origin for the length of one cell. Upper branch of superior anal appendage short, about one-half the length of lower branch, which is nearly equal in length to the lower appendage. Ac lies much nearer the level of Ax_2 than of Ax_1.

Head: upper surface entirely black; the upper lip polished, but without metallic reflex; lower lip grey-white; the rest of the under and posterior surfaces greenish white.

Prothorax: black above, grey-white below.

Synthorax: black above, no trace of antehumeral stripes; dark grey on the sides, a little pulverulent; paler below.

Abdomen: slender, but segments 7–10 distinctly stouter than 3–6. Bronze-black above, brownish white below. Anal appendages (see text-fig. 4) brown tipped with black.

Legs: grey-white, with black articulations and black lines on the posterior surfaces.

Wings: rather smoky; pterostigma almost square, but its inner margin more oblique than its outer; dark brown, very finely edged with lighter colour surrounded by a thickened black vein. Px 15.

Abd. 40+·5 mm., h. w. 23 mm.

Segments 3–6 of the abdomen measure 29·5 mm.

Comparison of this specimen with Ris's figures and examination with his diagnostic table (Ris, Nova Guinea, xiii. Zool. 2, pp. 100–102, fig. 22) has enabled me to determine that this species is not *T. superba* Selys, from which species it differs in its smaller size, absence of antehumeral stripes, and shape of anal appendages. My species, *T. kirbyi*, is unfortunately very imperfectly known, but on the whole the present specimen would seem to resemble it closely in colouring and venation, and it may, I think, be regarded as conspecific with it.

159. TEINOBASIS RAJAH Laidlaw.

Teinobasis rajah Laidlaw, Journ. Straits Branch R. Asiat. Soc. [63] 1912, p. 97.

2 ♂ ♂. Limbang, 22. vi. 11.

Thorax orange-red above, with median bronze-green stripe.

Abd. 33 mm., h. w. 20 mm.

Autotype ♂ in British Museum. Paratype ♂, coll. Ris.

160. STENAGRION DUBIUM (Laidlaw).

Pseudagrion (?) *dubium* Laidlaw, Journ. Straits Branch R. Asiat. Soc. [63] 1912, pp. 97–98, pl., fig. 5.

Stenagrion dubium id., Proc. Zool. Soc. London, 1915, p. 39; id., op. cit. 1917, p. 231 (fig. 10).

Legion PROTONEURA.

[I propose the following arrangement of the Oriental species grouped under the Selysian genera *Disparoneura* and *Caconeura* (*Alloneura* Selys). It is, I think, natural, and has the advantage of retaining many of the species in the original genera:—

A. Ac lies midway between ax_1 and ax_2.
  a. Posterior lobe of prothorax of female armed with hook-like projections.
    α. Ab meeting nerve descending from quadrilateral.
      i. Cu_1 reaching hinder margin of wings beyond half the wing-length .... *Chloroneura* Laidlaw.
      ii. Cu_1 reaching hinder margin of wings before half the wing-length .... *Disparoneura* Selys.
    β. Vestige of Ab not meeting nerve descending from quadrilateral, or absent altogether .... *Caconeura* Kirby.
  b. Posterior lobe of prothorax of female simple .... *Indoneura* Laidlaw.
B. Ac lies nearly at level of ax_1 or proximal to it .... *Risioneura* Munz.

Of these genera: *Chloroneura* appears to be confined to peninsular India; *Disparoneura* has a westerly range, extending from Africa to India and Burma and reaching its limit eastwards in Borneo: *Caconeura*, more specialized in some respects, extends from Burma to Malaya, with one species in Ceylon; whilst the still more specialized *Risioneura* is Papuan (see Laidlaw, Rec. Ind. Mus. xiii. 1917, pp. 343–344).]

161. CACONEURA DORSALIS (Selys).

Caconeura dorsalis Kirby, Cat. Odonata, p. 134.

Disparoneura dorsalis Laidlaw, Proc. Zool. Soc. London, 1913, p. 75.

3 ♂ ♂. Baram (*C. Hose*). 1 ♂. Murud, 18. xii. 14.

162. CACONEURA VERTICALIS (Selys).

Disparoneura verticalis Kirby, Cat. Odonata, p. 134; Krüger, Stettin. Entomol. Zeitg. 1898, p. 114; Förster, Fasc. Malay., Zool. iv. Odonata, Part II., (sep.) p. 14; Laidlaw, Proc. Zool. Soc. London, 1913, p. 75.

21 ♂ ♂, 3 ♀ ♀. Lio Matu, xi. 14. 2 ♂ ♂, 1 ♀. Retuh, 14. v. 14.

The presence of a vestige of Cu_2 is constant in all these specimens.

163. CACONEURA HYPERYTHRA (Selys).

Caconeura hyperythra Kirby, Cat. Odonata, p. 134.

Disparoneura hyperythra Laidlaw, Proc. Zool. Soc. London, 1913, p. 76.

164. CACONEURA HOSEI (Laidlaw).

Disparoneura hosei Laidlaw, Proc. Zool. Soc. London, 1913, pp. 76–78.

1 ♂. Baram (*C. Hose*), autotype, coll. F. F. L. 5 ♂ ♂. Lio Matu, 4. xi. 14. (1 ♂. Coll. Brit. Mus.)

165. CACONEURA PERAMŒNA (Laidlaw).

Disparoneura peramœna Laidlaw, Proc. Zool. Soc. London, 1913, pp, 76–77 (pl. iv. figs. 8, 8 *a*).

166. *CACONEURA INTERRUPTA (Selys).

Disparoneura interrupta Kirby, Cat. Odonata, p. 134.

167. *CACONEURA COLLARIS (Selys).

Disparoneura collaris Kirby, Cat. Odonata, p. 134.

Disparoneura notostigma collaris Förster, Fasc. Malay., Zool. iv. Odonata, Part II., (sep.) p. 13.

*[CACONEURA LANSBERGI (Selys).]

Caconeura lansbergi Kirby, Cat. Odonata, p. 134.

Location somewhat doubtful.

168. *CACONEURA GRACILLIMA (Selys).

Caconeura gracillima Kirby, Cat. Odonata, p. 131.

169. CACONEURA MOULTONI (Laidlaw).

Disparoneura moultoni Laidlaw, Journ. Straits Branch R. Asiat. Soc. [63] 1912, pp. 98–99.

1 ♂. Batu Lawi, 11. v. 11.

Upper lip pale yellow, with fine black margin, otherwise velvety black above. Dorsum of prothorax and synthorax black, a fine yellow lateral stripe on the latter. Abdomen brownish black.

No vestige of Cu_2; Cu_1 reaches first cross-nerve after the quadrangle in the fore-wing, the second in the hinder-wing; 14 postnodal costals in fore-wing.

Abd. 34 mm., h. w. 19 mm.

170. *DISPARONEURA AURANTIACA Selys.

Disparoneura aurantiaca Kirby, Cat. Odonata, p. 134.

171. DISPARONEURA ANALIS (Selys).

Disparoneura analis Kirby, Cat. Odonata, p. 134; Krüger, Stettin. Entomol. Zeitg. 1898, p. 111; Laidlaw, Sarawak, Mus. Journ. ii. no. 6, 1915, p. 275.

1 ♂. Baram, 29. iii. 10. 1 ♂. Saribas, 09. 1 ♂. Murud, 18. xii. 14. 1 ♂. Lio Matu, 1. xi. 14.

Legion PLATYSTICTA.

172. DREPANOSTICTA RUFOSTIGMA (Selys).

Platysticta rufostigma Kirby, Cat. Odonata, p. 133; Laidlaw. Proc. Zool. Soc. London, 1913, p. 79 (pl. iv. fig. 9).

(For definition of the genus *Drepanosticta*, see Laidlaw, Records Ind. Mus. xiii. part vi. p. 339 (1917).)

173. PROTOSTICTA VERSICOLOR Laidlaw.

Protosticta versicolor Laidlaw, Proc. Zool. Soc. London, 1913, pp. 78–79.

174. PROTOSTICTA KINABALUENSIS Laidlaw.

Protosticta kinabaluensis Laidlaw, Proc. Zool. Soc. London, 1915, pp. 37–38 (fig. 5, B).

Also 1 ♂ (imperfect), Mt. Merinjak, 26. v. 14, belonging to *Drepanosticta*, with the hinder margin of the thorax bilobed. Apparently an undescribed species.

Legion LESTES.

175. *LESTES WALLACEI Kirby.

Lestes wallacei Kirby, Cat. Odonata, p. 162.

Lestes sp.

1 ♂. Matang Rd., 21. viii. 20 (lacking head and end of abdomen).

Wings hyaline, but with smoky tinge, most marked at apex; petiolated up to level of Ac, which lies nearer Ax_2 than Ax_1. M_2 commencing $8\frac{1}{2}$–9 cells distal to nodus in fore-wing, $6\frac{1}{2}$–7 cells in hinder-wing. None of the sectors angulose except Cu_2. Pterostigma large, dilated, about four times as long as broad. One supplementary sector and vestige of a second interposed between M_2 and M_3. Quadrangle broad, lower side twice as long as upper side; outer angle acute.

This interesting species shows distinct affinities to the Indo-Chinese *Orolestes*.

There are also amongst Major Moulton's material some three fragmentary specimens, all Agrionines, which are too imperfect to describe. They appear to be unnamed species. One is a *Pseudagrion*; a second is either a *Pseudagrion* or belongs to an allied genus; the third I cannot refer with certainty to any genus, though again it may be related to *Pseudagrion*.

I have omitted from the list certain common and widely-spread species which almost certainly occur in Borneo, but which have never yet been recorded from the island. These would add some ten species or so to the list.

Allowing for these broken or unrecorded species, we may, I think, assume that the list includes from between 70 to 80 per cent. of the total Dragonfly fauna of the island.

III. *Some Remarks on Geographical Distribution.*

Dragonflies are so important in this respect that a few notes are not out of place.

It is difficult to subdivide the Oriental Region in any entirely satisfactory way; but one may contrast the equatorial Dragonfly fauna, ranging from about the equator to roughly 10° N., with the tropical fauna lying mainly between 10° N. and 25° N. The equatorial fauna may be called the Malayan, the tropical (unless, indeed, that can be shown to consist of more than one fauna of co-ordinate importance) I label here the Indo-Chinese.

The Malayan fauna occupies as its main areas:—

i. The Sondaic area—*i.e.*, the Malay Peninsula, Borneo, Sumatra, and Java.
ii. The Philippine Islands.
iii. The Celebes.

Any detailed analysis of the fauna of Malaya would extend this paper to undue length: hence I give only a very general table, and prefix "so far as I know" to the whole.

Table *of distribution of genera found in Borneo.*

I. Genera confined to Borneo.

Linæschna, *Pseudagrionoptera*, *Matronoides*, *Rhinoneura*, *Stenagrion*.

II. Genera specially characteristic of Malaya or confined thereto (several of these occur in Indo-China).

Tetracanthagyna, *Amphiæschna*, *Orchithemis*, *Pornothemis*, *Brachygonia*, *Tyriobapta*, *Micromerus**, *Dysphæa*, *Devadatta*, *Podolestes*, *Rhinagrion*, *Caconeura*, *Amphicnemis*, *Pericnemis*.

III. Genera of Oriental distribution, with species confined to Sondiac area.

Orogomphus, *Onychothemis*, *Macromidia*, *Azuma*, *Idionyx*, *Jagoria*, *Gomphidia*, *Leptogomphus*, *Macrogomphus*, *Microgomphus*, *Burmagomphus*, *Heterogomphus*, *Vestalis*, *Pseudophæa*, *Rhinocypha*, *Coliccia*, *Copera*. *Disparoneura*.

IV. Genera common to Oriental and Australian Regions, with species confined to Sondaic area.

Agrionoptera, *Neurothemis*, *Brachydiplax*, *Lyriothemis*, *Camacinia*, *Aciagrion*, *Drepanosticta*, *Protosticta*.

V. Genera mainly Papuan or Australian, with species confined to Sondaic area.

Metaphya, *Oda*, *Raphisma*, *Teinobasis*.

VI. Palæotropical (*a*) or Holotropical (*b*) genera, with species confined to Sondiac area.

(a) *Ictinus*, *Tetrathemis*, *Rhyothemis*, *Æthriamanta*, *Pseudagrion*, *Ceriagrion*.
(b) *Gynacantha*.

VII. Special cases :—

Hylæothemis.	Borneo, S. India, Ceylon.
Heliaeschna.	W. Africa, Malaya, Burma.
Macromia.	Palæotropical, Palæarctic, Nearctic.

Some negative characters showing contrast with Indo-Chinese Province :—

Absence of *Cordulegastrinæ*, relatively poor development of genera of *Calopteryginæ* and of *Brachytryon* series of *Æschninæ*.

Relative scarcity of species of the following genera :— *Onychogomphus*, *Lestes*, *Ischnura*, *Agriocnemis*.

Absence of *Davidius*, *Anisogomphus*, *Cyclogomphus*, *Gomphus*, *Pseudothemis*, *Sympetrum*, *Palpopleura sexmaculata*, *Bradinopyga*, *Anisopleura*.

Genera not mentioned in the above table have no species peculiar to the Sondiac area.

---

* *Micromerus* has 13 species in Malaya; one, *M. lineatus*, widely spread in Indo-Chinese province; and one, *M. finalis*, in Ceylon.

18. On some new Therocephalian Reptiles from the Karroo Beds of South Africa. By R. Broom, M.D., D.Sc., F.R.S., C.M.Z.S.

[Received April 13, 1920 : Read April 27, 1920.]

(Text-figures 1–9.)

Index.

Page
Ictidosuchus longiceps, sp. nov. 343
Alopecopsis atavus, gen. et sp. nov. 347
Moschorhinus kitchingi, gen. et sp. nov. 351
Whaitsia platyceps Haughton 354

Though more species and genera of Therocephalians are known than of either of the other two large suborders of the Carnivorous Therapsida—the Gorgonopsia and the Cynodontia,—the structure of the skull and skeleton is much better known in these later suborders. This is largely due to the fact that the Therocephalians are mainly found in the Lower Beaufort zones, where, owing to the petrological conditions, very fine complete specimens are rare. The Gorgonopsians which are found mostly in the *Cistecephalus* zone, and the Cynodonts which mainly occur in the Upper Triassic zones, are usually represented by well-preserved skulls with a matrix which can be fairly easily removed. Recently I have been fortunate in discovering one or two very interesting specimens of late Therocephalians formed in the Upper *Endothiodon* and *Cestecephalus* zones, which add considerably to our knowledge of the Therocephalian skull.

Ictidosuchus longiceps, sp. nov.

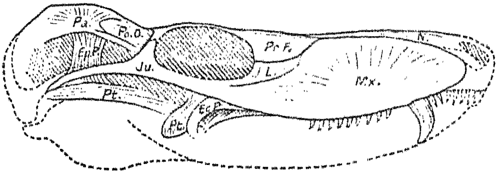
In 1900 I discovered near Pearston the remains of a very interesting type of Therocephalian which I described under the name *Ictidosuchus primaevus*. Until recently no other specimen of either this genus or species has ever been discovered, and as the type skull is very imperfect, a good specimen of this genus has long been one of our principal desiderata. In December 1917, I found at Bruintjeshooyte, between Somerset East and Pearston, a good skull, which may be referred to the genus *Ictidosuchus*, though a distinct species from *I. primaevus*.

The skull is nearly complete, lacking only the incisor portion, the occipital condyle, the arches of the left side and the quadrate region of the right. The palate is much weathered on the left side, but nearly perfect on the right.

As preserved, the skull measures in greatest length 135 mm., and when complete was probably 152 mm. long. The greatest breadth is about 84 mm. From the front of the orbit to the base of the canine is 52 mm., and from the front of the orbit to the front of the snout was probably about 75 mm. The inter-orbital measurement is 22 mm., and the antero posterior measurement of the orbit is 32 mm.

The premaxillæ and septomaxillæ are lost. The nasals are long and narrow, only slightly wider in front and behind than in the middle region. The maxilla is unusually long in comparison with its depth. It passes forwards a considerable distance in advance of the canine and backwards much beyond the last molar. In front of the main canine there are two small canines as in *Scaloposaurus*, but the present type, besides differing very greatly in many other ways, differs in having the third tooth developed into a powerful canine. The canine here measures about 15 mm. in height and 5 mm. in antero-posterior length. It is usually curved, and is remarkable for having no serrations along its posterior border. The three canines together measure 9·5 mm. Behind the main canine is a diastema of 6·5 mm. followed by a series of 9 small cone-like molars, the whole molar series measuring 25 mm. In *Ictidosuchus primævus* there are apparently only 8 molars, but as both the upper and lower jaws are badly preserved, it is not improbable that there may also have been 9 in the type species. The molars of *Ictidosuchus primævus* are considerably larger and closer together, but appear to be otherwise similar to those of *I. longiceps*.

Text-figure 1.*



Side view of skull of *Ictidosuchus longiceps* Broom.

The prefrontal is a relatively large bone which forms the anterior half of the upper orbital margin and extends down to the middle of the anterior border. The lacrimal is considerably less than half the size of the prefrontal, as will be seen in the figure given.

The jugal is a very long slender bone forming most of the sub-orbital bar and about half of the outer temporal arch. A strong but short ascending process forms the lower half of the post-orbital arch, articulating with the short postorbital bar of the postorbital bone.

The frontals are relatively small, and only form a very small part of the supraorbital margin. The bones are about the same length as the orbit, and articulate in front with the nasals by an irregular transverse suture, and posteriorly with the parietals by a transverse serrated suture.

---

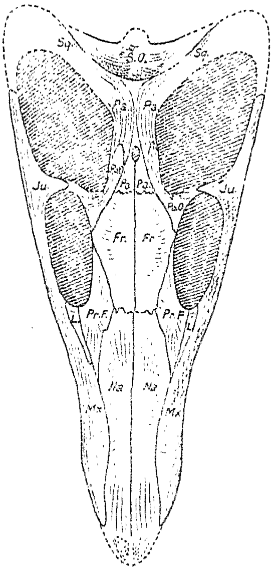
* For explanation of lettering, see p. 355.

There is no postfrontal.

The postorbital is relatively small, forming the posterior half of the upper orbital margin and the upper half of the postorbital arch. It extends backwards by the side of the parietal to the plane of the posterior border of the pineal foramen.

The parietals are relatively long and slender. In front they are flattened out, and form a transverse suture with the frontals. Posteriorly they form a sharp intertemporal crest, and at the front of the crest is a large oval pineal foramen. From the posterior part of the crest the parietals pass outwards, forming a considerable part of the occipital crest.

Text-figure 2.



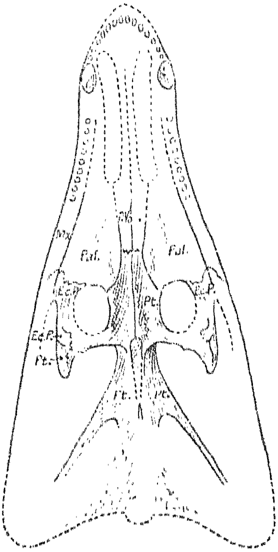
Upper surface of skull of *Ictidosuchus longiceps* Broom.

The occiput is very imperfectly preserved. It is shallow and broad, and from the upper margin of the foramen magnum the bone passes upwards and forwards. The elements cannot be clearly made out, though they are doubtless as in better-known Therocephalians. The squamosals and quadrates are lost.

As already stated, the palate has not been fully cleared in front as the matrix is required to support the teeth, but the structure is sufficiently revealed in all the posterior part. A transverse fracture through about the plane of the third last molar shows in section the prevomers. Though very closely placed to each other they are not anchylosed. Each has an ascending thin plate and a short descending plate, and from each bone a transverse plate passes outwards which approaches and doubtless further back meets the palatine. The palatines as seen here in section are slender curved bones which below meet the maxillaries, and on passing inwards and then upwards again approach and possibly meet the upper borders of the maxillaries.

The prevomers extend backwards a considerable distance behind the plane of the last molars and meet the anterior ends of the pterygoids. The palatines form the greater part of the bony roof of the mouth, passing about as far back as the posterior end

Text-figure 3.



Palatal surface of skull of *Ictidosuchus longiceps* Broom.

of the maxilla. There is behind the palatine a large suborbital vacuity as in *Scylacosaurus*, and, as in that genus, this vacuity is bounded externally by the ectopterygoid. The ectopterygoid is moderately slender, but in front of the pterygoid process which lies along the inner side of the mandibles it has a well-developed descending process, which adds much support to the pterygoid process.

The pterygoid is fairly similar to that already described and figured by me in *Scylacosaurus*, and possibly some of the apparent differences may be due to certain features being preserved in the present specimen which were lost in the other. As in most primitive reptiles, there is an anterior process which, passing inside of the palatine, meets the prevomer; an outer descending process which forms the posterior border of the suborbital vacuity and has a long articulation with the ectopterygoid; and a long posterior process, the inner part of which apparently articulates with the basisphenoid, and the outer branch of which doubtless passes back to meet the quadrate. Though the posterior process is almost perfectly preserved, as the quadrate is lost the mode of articulation is not seen. An interesting point about the pterygoid is that there are no teeth on it. Near the posterior part of the anterior palatine process there is in the middle line a prominent median spur formed by the two bones meeting, and immediately behind this is a moderately large median vacuity. At the inner end of the outer process is a well-marked descending spur, the exact length of which is unknown as it is broken off near the base.

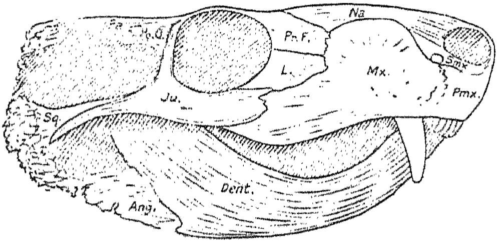
Above the outer branch of the posterior process is seen the well-developed epipterygoid. This differs from that figured by me in *Scylacosaurus* (Phil. Trans. 1915) in having a shorter and broader upper portion and a differently shaped basal, which lies in the pterygoid as seen in the figure given.

The basicranial region is too much weathered to be worth describing in detail.

ALOPECOPSIS ATAVUS, gen. et sp. nov.

This new genus and species is founded on a nearly complete skull discovered by me at New Bethesda, and it is of much importance as revealing another new type of Therocephalian.

Text-figure 4.



Side view of skull of *Alopecopsis atavus* Broom.

The specimen is in rather indurated shale, and as the bone is more friable than the matrix, complete development is difficult, and it has been considered advisable to leave a fair amount of matrix on the specimen. Enough has, however, been undertaken to show most details of the structure. The whole of the right side of the skull is preserved except a part of the quadrate and squamosal regions, and the right mandible is in position. The left side has lost the greater part of the jugal and squamosal, and the left mandible has been completely detached and lost before fossilisation.

The skull as preserved measures 198 mm. and was probably about 202 mm. in greatest length. The greatest width across the squamosals has been about 90 mm. From the front of the snout to the front of the orbit is 90 mm. The greatest width of the snout in the canine region is 45 mm., and the narrowest measurement between the supraorbital edges is 39 mm.

The premaxilla is relatively small, and is much overlapped by the maxilla. It sends upwards between the nostrils a slender internasal process to meet the nasal above. Most of the teeth are lost, but portions of three are stil seen, and from the sockets the number and size of all can be determined. There is evidence of six incisors, of which the 6th is very small. The whole six measure 24 mm. At the front end of the premaxilla are two moderately large foramina for branches of sensory nerve—presumably a branch of the second division of the Vth.

The septomaxilla lies along the outer border of the nostril, and passes backwards a short distance between the nasal and maxilla. Between the septomaxilla and maxilla there is, as in other previously known early carnivorous Therapsids, a large foramen, the significance of which is at present unknown. In most fœtal mammals there is a large gland duct developed along the outer side of the nasal cavity, which from its very early development is evidently the remains of some structure once of much greater importance. It seems not improbable that this large foramen, which passes into the nasal cavity between the septomaxilla and maxilla and is continued as a wide groove for some distance upwards and backwards along the upper border of the maxilla, was for the lodgment of the glandular and possibly sensory organ whose rudiment is met with in most mammals.

The nasal is long and narrow, but broader at each end than in the middle. The shape and relations will be best understood from the figures given.

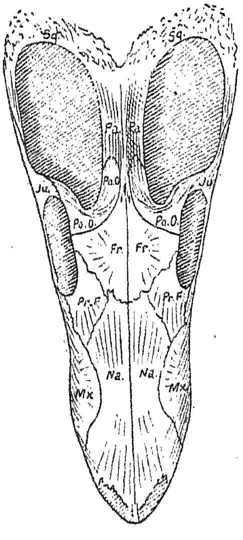
The maxilla is a powerfully developed bone of considerable depth. There is a single large canine which unfortunately is not well preserved on either side. In front of the elevation which accommodates the root of the canine, the maxilla overlaps the premaxilla as in most Therocephalians, and in the anterior part of the bone are three fairly large foramina, presumably for branches of the Vth nerve. In the canine region the surface of the bone is considerably pitted, probably by glands in the skin, and there are a number of small openings, apparently for nerves. The maxillary branch of the Vth nerve apparently passes into the maxilla by a large foramen on the inner side of the bone behind the canine, and passing forwards outside the canine, comes to the surface through the numerous small foramina in the front of the bone. Behind the canine there is a long slender alveolar margin, which is remarkable in having no trace of molar teeth. In many skulls when no molars are found we suspect that they may have been lost, but here this can hardly be the case. Both maxillæ are well preserved and the dentary as well, yet in none of the three bones is there any trace of molars. Further, the alveolar margin is narrow and sharp, and would be much too slender for the accommodation of molars large enough to be serviceable to an animal of the size.

The lacrimal is fairly large, and forms a considerable part of the facial surface, which is very smooth.

The prefrontal forms the anterior and upper quarter of the orbital margin. It meets the frontal, nasal, maxilla, and lacrimal bones.

The frontals are relatively small, and the two form most of the slightly concave interorbital surface. In front each has a short articulation with the nasal and a much longer oblique articulation with the prefrontal, and as the prefrontal nearly extends backwards to the postorbital, the frontal only forms a very small part of the orbital margin. Posteriorly the frontal has a long articulation with the postorbital, and a short interdigitating suture with the parietal mainly hidden by the postorbital.

Text-figure 5.



Upper surface of skull of *Alopecopsis atavus* Broom.

There is no postfrontal.

The postorbital is a peculiarly twisted bone. Its inner end lies against the narrow parietal crest, and from this, passing directed mainly antero-posteriorly. The posterior two incisors are more rounded.

The septomaxillary is large, and forms the lower border of the nostril, but does not extend far backwards between the nasal and the maxilla. The foramen, usually present between the septomaxilla and maxilla, is small.

The nasal bone is exceptionally large and broad. In front it is crushed down on the nostrils and the details of structure cannot be made out, but doubtless the arrangement is similar to that in typical Therocephalians. Posteriorly the nasal meets the frontal a little in front of the plane through the centre of the orbit. The shape of the bone will be best understood from the figure.

The maxilla is a short but powerful bone. It overlaps the premaxilla to between the roots of the 3rd and 4th incisors. It has one large canine which measures 20 mm. × 12 mm. Behind the canine only a very small part of the maxilla shows on the palatal aspect, and in the specimen there are no teeth, but on each side there are indications of two old sockets with a possible third very small one; and I think we may assume that there were three molars, of which the 3rd was small. The three would measure about 19 mm. The upper dental formula would thus be i.^{6}, c.^{1}, m.^{3}

The prefrontal is relatively small, and wedged in between the nasal and frontal above and the maxilla and lacrimal below.

The lacrimal is slightly larger than the prefrontal, and it forms most of the front of the orbit. Near the middle of the bone and on the orbital margin is a well-developed bony boss, and on the inner side of this and near its upper end is a large lacrimal foramen.

Very little of the jugal is preserved, but the part underneath the orbit forms with the maxilla a very deep and powerful suborbital arch.

The frontals are large and wide, as seen in the figure.

There is no postfrontal. The postorbital lies on the frontal and parietal.

The parietal crest is narrow as in typical Therocephalians, but the pineal foramen is rudimentary.

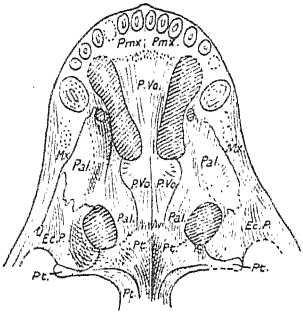
The palate is beautifully preserved and remarkably interesting. The palatal portion of the premaxillaries has not been displayed as the matrix is required to support the fragmentary incisors.

The prevomers form a large part of the bony roof of the mouth. In front they are anchylosed and form a wide plate between the internal nares. At the back part of the nares they are much constricted, but beyond this widen out again into a fan-shaped structure which lies between the palatines and meets the pterygoids. In this back part a median suture between the two prevomers is very distinctly seen.

The palatine is a large and powerful bone. Externally it has a long articulation with the maxilla, and here the palatine is so thickened that it forms more of the wide alveolar surface than does the maxilla. In front and nearly on the plane of the back of the canine, where the maxilla passes up to form the vault of the palate, the palatine lies closely against the maxilla except where there is a large foramen, presumably for a nerve. Haughton figures two foramina in a corresponding structure in *Akidognathus*. Near the middle of the palatine is an oblique ridge, which probably supported a soft palate and carried the internal nares back to the anterior pterygoid region. The inner side of the palatine articulates with the prevomer and the pterygoid. The greater part of the posterior border forms the margin of the suborbital vacuity. Further out is a moderately large articulation with the ectopterygoid.

The ectopterygoid is an irregularly shaped bone, not unlike a bird's quadrate. Anteriorly it articulates with the palatine; externally with the maxilla and probably with the jugal. Between the maxilla and the ectopterygoid is a small foramen. Posteriorly there is a large flat articulation between the ectopterygoid and the pterygoid. In front of the pterygoid process there is an even larger ectopterygoid process. All the outer side of the suborbital vacuity is formed by the ectopterygoid and much of the posterior.

Text-figure 8.



Palate of *Moschorhinus kitchingi* Broom.

Only the anterior portions of the pterygoids are preserved. From the broad deep lateral portions which articulate with the ectopterygoids they pass forward only a comparatively short distance to meet the prevomers and the palatines. In this region each pterygoid sends down a thin vertical plate, which, uniting with its neighbour, forms a median keel.

In general structure the palate agrees more closely with that in *Akidognathus*, though the proportions of the bones are very different. In *Akidognathus* the prevomers have, as in *Moschorhinus*, a suture between them, and yet are anchylosed in front. *Moschorhinus* differs in having no interpterygoid vacuity so far as can be seen in the specimen. If one be present, it must be much further back than in *Akidognathus*.

There is another palate recently discovered with which a comparison may be made—viz., *Whaitsia platyceps*. This new type was recently described by Haughton, and though it differs greatly from *Moschorhinus*, the snout has so much superficial resemblance that a comparison seems advisable, even if only to clearly differentiate the types. *Whaitsia* is a large Therocephalian—one of the largest known. It has a broad flat snout, and if it were not for the great difference in the palate, one might be inclined to think that *Moschorhinus* was a near ally. Further, in the type of *Whaitsia* the number of incisors cannot be made out, though there are four in what is regarded as a co-type. The palate, however, is so very unlike that of any form previously known that Mr. Haughton very wisely puts *Whaitsia* in a new family—the Whaitsidiæ.

Text-figure 9.

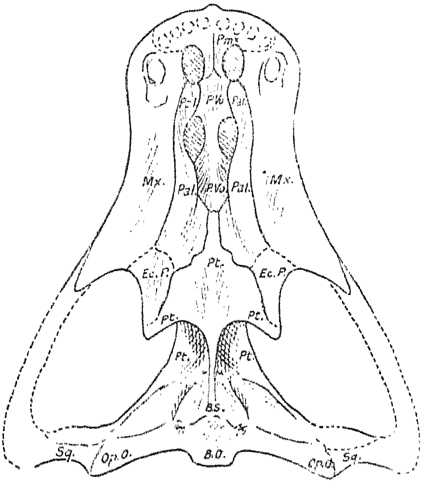


Diagram of palate of *Whaitsia platyceps* Haughton.

Mr. Haughton has given an excellent description of the type and a figure of both upper and lower sides. The description he has given is so accurate that little need be added to it. But the figure he gives of the palate is not very clear, and a new and independent figure of this unique palate may not be regarded as superfluous.

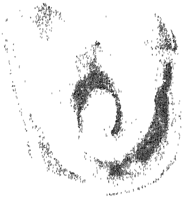
If the palate, as I figure it, be compared with that of *Moschorhinus*, it will be seen to differ in only two important points. The suborbital vacuity, which in all typical Therocephalians is large, is here practically closed, and the back part of the palate is thus made to resemble slightly that of the Gorgonopsia. In front, instead of there being a pair of large openings as in all other known Therocephalians, there are four openings. If the anterior part of the palate be compared with that in *Moschorhinus*, it will be seen that the difference is that the anterior ends of the palatines pass inwards, and meet the prevomers dividing what were large internal nares into anterior and posterior portions—the posterior alone being, as Haughton has suggested, the internal nares. What has happened is exactly comparable to what has happened with the external nares in *Chamæleon*, where the original opening becomes divided into two by the prefrontal passing forwards.

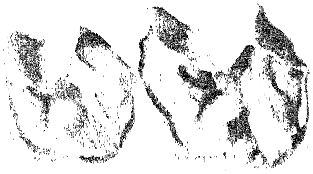
Haughton discusses the affinities of *Whaitsia* with Therocephalians, Gorgonopsians, and Cynodonts, and inclines to regard it as a highly specialised Gorgonopsian, but it seems to me that it is a true but aberrant Therocephalian.

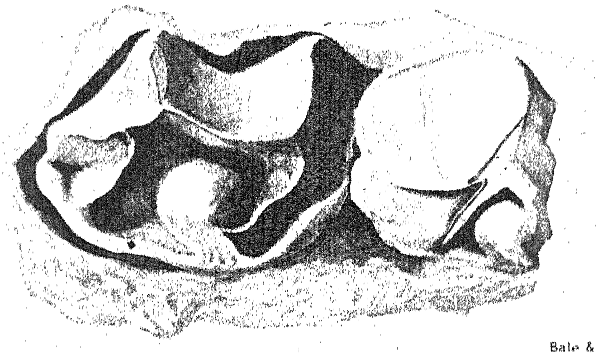
References to lettering.

Ang. Angular; *B.O.* Basioccipital; *B.S.* Basisphenoid; *Dent.* Dentary; *Ec.P.* Ectopterygoid or Transpalatine; *Ep.P.* Epipterygoid; *Fr.* Frontal; *Ju.* Jugal; *Mx.* Maxilla; *Na.* Nasal; *OpO.* Opisthotic or Paroccipital; *Pa.* Parietal; *Pal.* Palatine; *Pmx.* Premaxilla; *PrF.* Prefrontal; *PoO.* Postorbital; *Pt.* Pterygoid; *P.Vo.* Prevomer; *Smx.* Septomaxilla; *Sq.* Squamosal; *Vo=Pa.S.* Vomer=Parasphenoid.

P. Z. S. 1920, FORSTER-COOPER, Pl. I.







Bale & Danielsson, Ltd.

CHALICOTHEROIDEA from BALUCHISTAN.

19. Chalicotheroidea from Baluchistan. By C. Forster-Cooper, M.A., F.Z.S., Superintendent of the University Museum of Zoology, Cambridge.

[Received April 16, 1920: Read May 11, 1920.]

(Plate I.* and Text-figures 1-7.)

Dr. Pilgrim, in his report † on the fossil vertebrate fauna of the Bugti Hills, has described two forms of Chalicotheres, of which the smaller is represented by material too fragmentary to be named, while to the larger he has given generic rank with the name of *Phyllotillon naricus*.

My own collections have produced a small amount of further material for study, fragmentary and in some cases much worn, but sufficient to add in some points to our knowledge of these two forms.

Holland and Peterson ‡ in their very complete memoir on *Moropus elatus* and the osteology of the Chalicotheroidea have taken exception to the creation by Dr. Pilgrim of a separate genus for his species, *Phyllotillon naricus*. This objection is reasonable, seeing that the chief character on which the genus is founded is one which occurs in other genera of Chalicotheres. Dr. Pilgrim states § that "the difference is particularly well shown in the structure of the upper premolars. . . . An unworn specimen of pm. 3 . . . . shows that the large inner cusp was united to the ectoloph by a double instead of a single crest." This statement, as Holland and Peterson point out, is open to alternative interpretations—viz., either that there is a crest running from each side of the inner cusp to the ectoloph, or that each crest is double.

The former interpretation represents the actual condition of the tooth, and is the meaning Dr. Pilgrim wished to convey ‖. As this condition is found in *Moropus* it loses its value as a generic character. On the other hand, to judge from Dépéret's figure of *Macrotherium grande* ¶, the fourth premolar does appear to differ in the arrangement of the crests from that of the Bugti specimens in that the anterior crest seems less developed in *M. grande*, in which form the anterior external cusp is a separate rounded hillock. Gaudry's figure of *Schizotherium modicum* shows both

---

[*] For explanation of the Plate, see p. 366.

[†] Rec. Geol. Surv. Ind. xl. p. 67, and Mem. Geol. Surv. Ind. n. s. vol. iv. Mem. 2, p. 33.

[‡] Mem. Carnegie Mus. vol. iii. no. 2, 1913.

[§] Mem. *loc. cit.* p. 33.

[‖] I had the opportunity of consulting Dr. Pilgrim on this point during a short visit made by him to Cambridge, and have his authority for making this statement.

[¶] Arch. du Mus. d'Hist. Nat. de Lyon, vol. v. 1892, pl. iii. fig. 1.

ridges, but the anterior seems to be weaker than the posterior, while the preceding premolars seem to have no anterior ridges. *Chalicotherium sivalense* is like *Schizotherium* in this respect, according to Falconer's figures in the 'Fauna Antiqua Sivalensis,' plate lxxx.

There are other differences from *Macrotherium* in the shape of the various teeth, so that there are some grounds for Dr. Pilgrim's separating them.

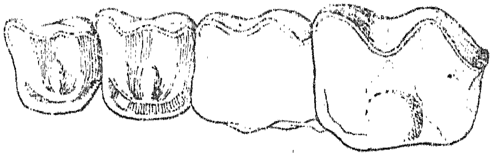
Whether or not the Bugti specimens can be placed in any other described genus is even more difficult to decide. Our combined material is scanty and none too well preserved, so that many characters remain unknown or at best uncertain, and for the present it seems useful to retain the generic name of *Phyllotillon*.

The material forming the basis of the present description consists of :—

1. A series of upper teeth, pm. 3–4, m. 1–2, much worn but giving the outline and general shapes of the teeth.
2. A moderately worn third and fourth upper premolar.
3. Three separate upper molars.
4. A fourth upper premolar only a little worn.
5. Fragmentary lower molars and lower jaws, sufficient when combined to give an outline of the middle portion of the mandible.
6. Some separate toe bones.

The first and second specimens (text-fig. 1) supplement Dr. Pilgrim's figure * in giving a better preserved shape of pm. 3 and in adding the shape of the second molar. The third premolar as well as the fourth (this outline filled in from the second specimen) have, roughly speaking, a square outline; the anterior outside border is produced into a somewhat prominent style, more pronounced than in *Macrotherium* and to much the same degree as in *Moropus*. In proportions the teeth differ from other described

Text-figure 1.



Phyllotillon naricus. 3rd and 4th premolars, 1st and 2nd molars. × ½.

---

* Mem. *loc. cit.* pl. xii. fig. 2.

forms in the greater approximation of the length and breadth, being square rather than transversely elongated.

The upper figure in Plate I. represents the fourth upper premolar in a slightly worn condition, and illustrates the two ridges described by Pilgrim; in the centro-internal cusp and broad internal cingulum it shows features characteristic of all Chalicotheroids.

The molars are all elongated, and in this respect differ from those of *Macrotherium*, where they are all square, and from *Nestoritherium* and *Circotherium*, where the molars change from square in the front one to elongate in the third. They agree best with those of *Moropus*, but carry the elongation to a still greater degree, and represent the greatest modification in this respect.

The lower figure in Plate I. shows two right upper molars just erupted, only the posterior half of the second being preserved. The condition of this fragment is excellent. In shape and in pattern they resemble Dépéret's figures* of the milk teeth of *Macrotherium* and also those figured by Pilgrim for this species †. They are, however, in all probability the permanent second and third molars, being considerably larger than the measurements of the milk teeth given by Pilgrim—*i. e.*, the third molar is 48 mm. long and 36 mm. wide in the front half as against 40 mm. and 31 mm. The only points in which these teeth differ from Pilgrim's description of his specimen are that here the whole external surface of the metacone—*i. e.*, from mesostyle to metastyle—is considerably smaller in the third molar than in the second, and that faint ribs are present on the external surface of the metacone of the second tooth and quite absent on that of the third. A corresponding rib, rather more clearly marked, is present on the paracone external surface of the third molar, and presumably would be found in the other molars. These ribs are not shown in Dépéret's figures ‡, and in Holland and Peterson's figures of *Moropus* they are shown only on the protocones of all three molars, where, however, they appear to be strongly marked.

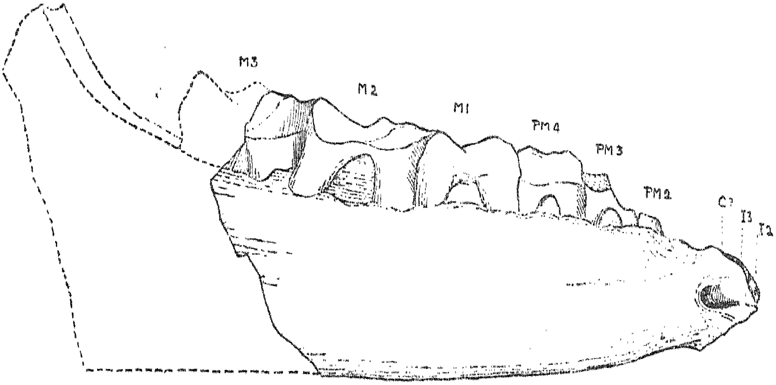
Text-fig. 2 shows the outline of one of the fragments of mandible which has the socket for three incisors, or the second and third incisor and a canine—all apparently small-rooted teeth—and the whole premolar-molar series except the last half of the third molar. This is continued by another fragment (the dotted outline in the figure) with the third and the second half of the second molar. As these fragments coincide in size they may be considered as belonging to the same species.

The mandible thus reconstructed shows certain peculiarities. Compared with the best-known Chalicothere (*Moropus elatus*), as figured by Holland and Peterson §, it has a much flatter lower border and is without the swelling under the anterior premolar. There is evidence, however, of a similar swelling further forward, which in this jaw is just under the mental foramen. This point marks the beginning of the symphysis, and the lower border in the region just behind the symphysis is sharp and ridge-like. There is apparently only one mental foramen instead of several, but it is much larger in proportion than those of *M. elatus*. The diastema between the incisor and anterior premolar is small (circa 25 mm.), and the latter tooth seems to have been very much reduced in size. The jaw is about half the length of *M. elatus*, while the teeth are nearly as big, so that the proportions are entirely different. The hinder part of the jaw is not known, but in the fragments at hand there is no sign of a downwardly-turned angle, though Pilgrim's figure* suggests a slight one.

---

* *Loc. cit.* pl. iii. figs. 4 & 5.
† Mem. pl. xii. fig. 3.
‡ *Loc. cit.*
§ *Loc. cit.* pl. lii.

Text-figure 2.



Phyllotillon naricus. Fragment of mandible with dotted outline of another fragment in continuation. × ½.

The flat lower border is a point of difference from *Macrotherium rhodanicum* and other forms in which this feature is known, while the shortening of the anterior part is a point in common with *M. rhodanicum* and *Chalicotherium sivalense*.

The subjoined measurements show that the animal occurred in two sizes, which possibly represents a sexual difference:—

---

* *Loc. cit.* pl. xii. fig. 4*a*.

Upper Teeth.

Premolars.				*Molars.*								
Third.		Fourth.		First.			Second.			Third.		
Length	Breadth	Length	Breadth	Length	Breadth: front	hind	Length	Breadth: front	hind	Length	Breadth: front	hind
23	23	25	26	—	—	—	—	—	—		—	—
23	?	25?	27	32	?	30?	17	37	35	—	—	—
—	—	—	—	—	—	—	?	?	35	48	36	34
							Three separate molars ? 2nd or 3rd			41	31	30
										41	34	29
										41	32	28
Lower Teeth.												
19?	?	23	15	30	16?	16?	42	21	22?	?	22	?
—	—	24	15	28?	16	18?	40	21	21	46	23	23
23	13	24	15									
										44	22	21
										51	25	24

Measurements in millimetres.

A few toe bones found in these deposits are noticed at the end of this paper. They show certain characters of interest, but as they may be the smaller toes of this species or the larger ones of the following, they are of no specific value.

The main characters of this form may be summarised as follows:—

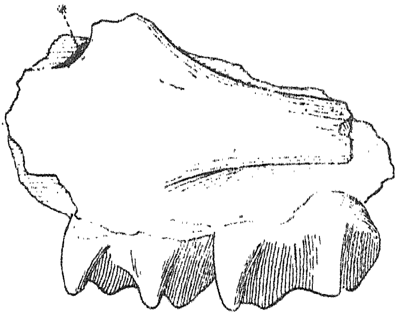
Dentition $\frac{3}{3}\cdot\frac{1}{1}$ or $\frac{0}{0}$, pm. $\frac{3}{3}$, m. $\frac{3}{3}$. Upper premolars square. Lower pm. 2 small (pm. 1 absent above and below). pm. 3 & 4 elongate. All molars elongate, especially the second. Lower border of lower jaw unusually flat: one mental foramen. Jaw in section rather flat outside and slightly convex inside. Moderate diastema in front of anterior lower premolar. There is thus a mixture of various generic characters, the balance, perhaps, favouring a general resemblance to *Moropus*. The form is at present insufficiently known, but there is enough to warrant the retention of Dr. Pilgrim's generic name until further material is discovered.

SCHIZOTHERIUM PILGRIMI, sp. n.

Pilgrim also mentions the presence of a smaller form in these deposits, indicated by some fragments too much worn for accurate description. In the present collection are two unworn and perfectly preserved upper molars (Plate I., central figure) of an animal much smaller than those of the species just described, and which may belong to Pilgrim's undescribed species although even a shade smaller than the latter.

The smaller size of these teeth suggests at first that they are milk teeth, but there are certain arguments against this view, which is not adopted here. The specimen fortunately has just enough of the anterior part on the zygomatic arch to show the relative position of the teeth in the maxilla (text-fig. 3). A reference to Holland and Peterson's figure * shows that in the milk and permanent molars of *Moropus* the last milk tooth lies well in front of the anterior root of the maxillary process of the zygoma, the first molar under the root of this process, and the second under its posterior border. If the present specimen is grown in a similar way, it supports the view that the teeth are the first two true molars. The anterior tooth is slightly worn, the second only just erupted. Beneath them there are cavities without trace of successional teeth and too small to allow of them. The teeth being fully formed and practically in wear, the germs of the succeeding teeth would have been comparatively well developed.

Text-figure 3.



Schizotherium ? pilgrimi. 1st and 2nd upper molars in side view, showing their position relative to the zygomatic arch. The position of the antorbital foramen is marked with an *. Nat. size. Type-specimen.

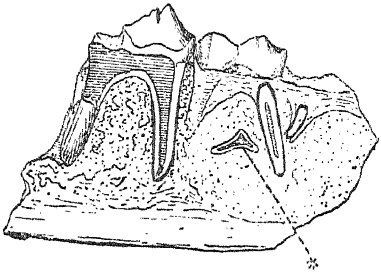
Moreover, of two fragments of lower jaws one has the last milk molar fairly well worn and the front part of the first lower molar just erupted. One side of this specimen has been ground away, and the section (text-fig. 4) shows the last milk molar with the section of the edge of the permanent succeeding tooth below it; there is no germ below the next tooth, whose roots are much larger and straighter. This tooth fits the front tooth of the two upper molars mentioned above.

---

* *Loc. cit.* pl. li. figs. 1-2.

A second specimen shows two lower molars well worn, of which the first is about the same size as the first true molars of the previous specimen. The fragment is broken away underneath, and the roots show that they belong undoubtedly to permanent teeth.

Text-figure 4.



Schizotherium ? pilgrimi. Fragment of lower jaw with last deciduous tooth and 1st true molar. One side of the specimen is ground away, showing the edge of the germ of the 4th premolar, marked with an *. The anterior root of the deciduous tooth is in section, the level of the posterior root not being quite reached by the grinding. The stout front root of the 1st molar is in section, the posterior is partly in section and partly a cavity: *i. e.* the lower half, where the root has fallen out. Nat. size.

The upper dentition being the best preserved is here made the type-specimen of the species.

Measurements (in millimetres):—

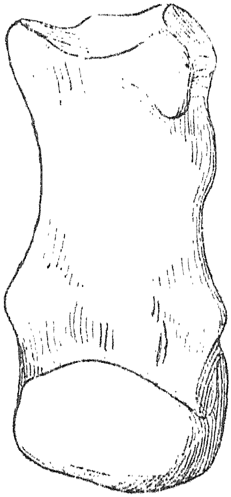
Upper molars.	Type-specimen.	
	1st molar.	2nd molar.
Length	21	25
Breadth, front half ...	20	24
,, second half..	20	23

Lower molars.	1st.	2nd.	1st.	2nd.
Length	18	—	18	22
Breadth, front half ...	10	—	10	12
,, second half...	?	—	11	12
Figured specimen (text-fig. 4).			Second specimen.	

The upper molars are square, and resemble those of *Schizotherium modicum* in size as well as in shape. The attribution of the present species to the genus is tentative.

There is yet another specimen of a lower jaw with a much worn first molar and roots of the last premolar and second and third molars. The first molar is 22 mm. long and about 12 mm. broad, and is therefore larger than the other specimens. The lower border of the jaw is extremely straight, as in *Phyllotillon naricus*. In size it seems to correspond with Pilgrim's unnamed fragment. Whether it represents a sexual difference from *Schizotherium pilgrimi* or yet a third species remains unsolved.

Text-figure 5.



? Metacarpal or metatarsal of a Chalicotheroid. Nat. size.

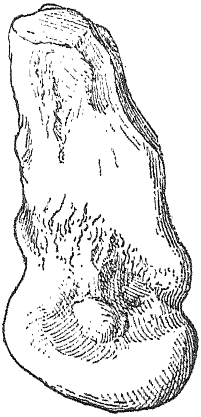
Until the anatomy of these animals, and indeed of all Chalicotheres with the exception of *Moropus*, is better known, it is impossible to feel sure of their generic position. A good deal of interest lies in the condition of the feet and the gradual loss of the first and fifth toes. According to Holland and Peterson *, both should be present in the fore foot of the *Schizotheriinæ*. In the present collection are several phalanges and one bone which may be a lateral podial (text-fig. 5); it is just possible that it may represent a fifth metacarpal or tarsal. Of the phalanges three out of six show the co-ossification of the proximal and median (text-fig. 6), which was evidently a common feature, as Holland and Peterson describe it in *Moropus*. The free proximal phalanges all show strongly-marked tubercles on the posterior faces (text-fig. 7) for the flexor attachments. Some of the fused bones show this feature, but to a less degree. They are not to be found in corresponding bones of *Macrotherium* or

---

* *Loc. cit.* p. 201.

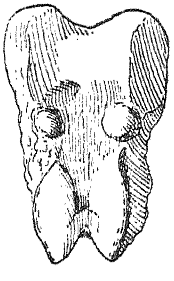
Chalicotherium in the British Museum collection, nor have they been noted or figured elsewhere. It is not possible at present to assign these bones to one or other of the Baluchi species.

Text-figure 6.



Co-ossified proximal and median phalanges of a Chalicotheroid, lateral surface. × ½.

Text-figure 7.



Median phalanx of a Chalicotheroid, posterior surface showing the two tubercles. × ½.

It is interesting to note that while remains of Anthracotheres and Rhinoceroses of all kinds are very abundant in the Dera Bugti deposits, Chalicothere remains are here, as elsewhere, extremely rare. They seem to have been of solitary as well as of strange habits, though recent discoveries seem to point to *Moropus* having been to some extent gregarious.

Note.—The specimens mentioned in this paper together with all the other Chalicothere material from Baluchistan have been added to the British Museum collections.

EXPLANATION OF PLATE I.

UPPER FIGURE.

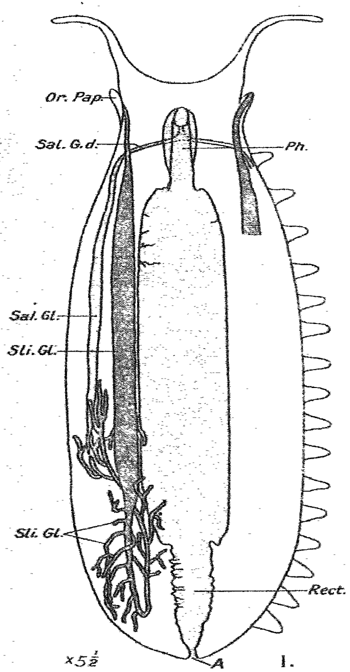
Phyllotillon naricus. 4th upper premolar. Nat. size.

LOWER FIGURE.

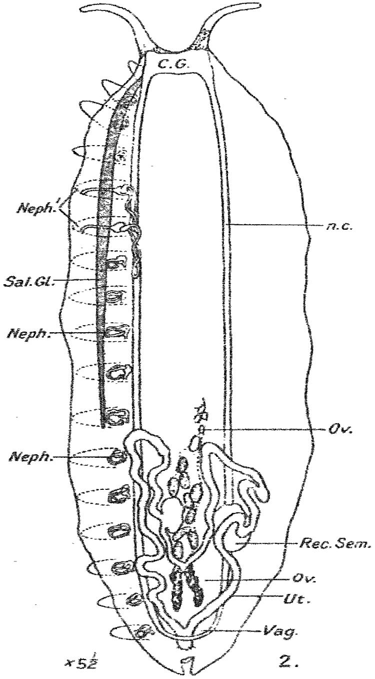
Phyllotillon naricus. 3rd upper molar and part of 2nd. Nat. size.

CENTRAL FIGURE.

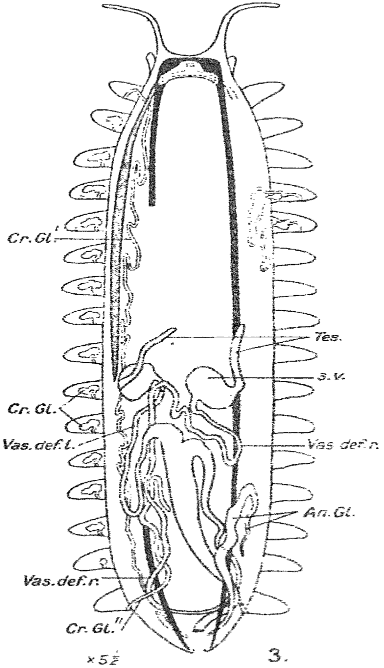
Schizotherium ? pilgrimi. 1st and 2nd upper molars. Nat. size: type-specimen.



1.

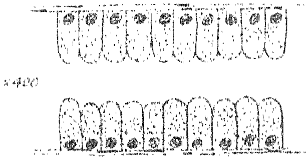


2.

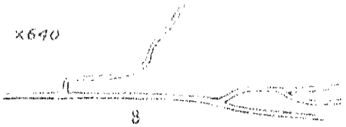


3.

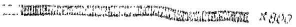
WEST AUSTRALIAN PERIPATOIDES.



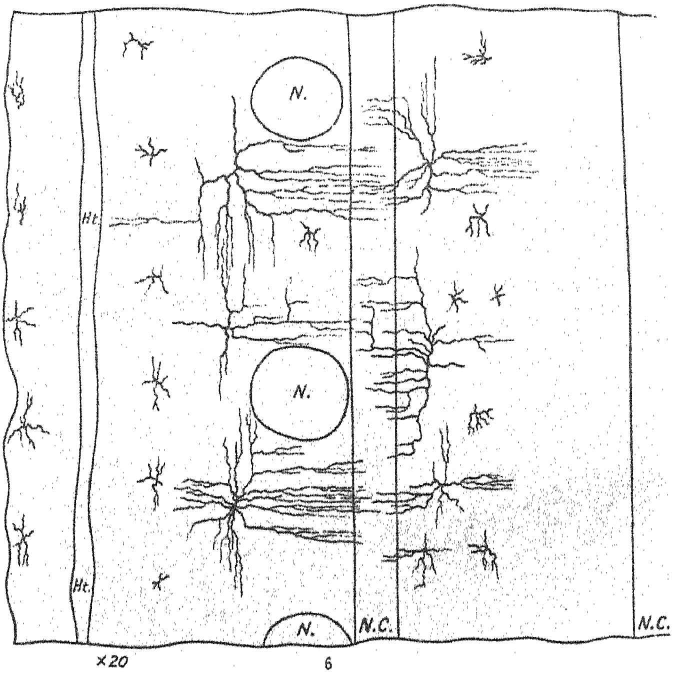
5



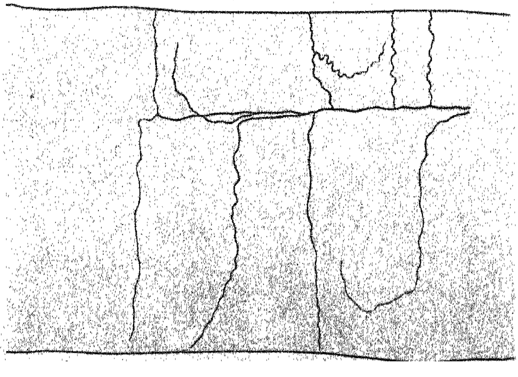
8

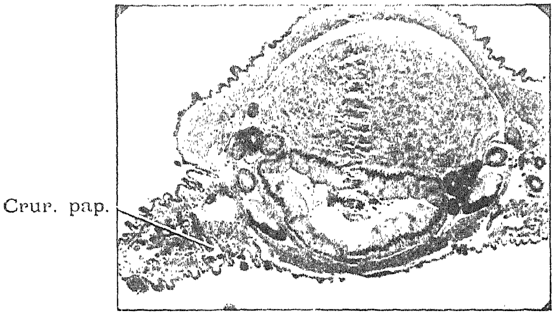


9

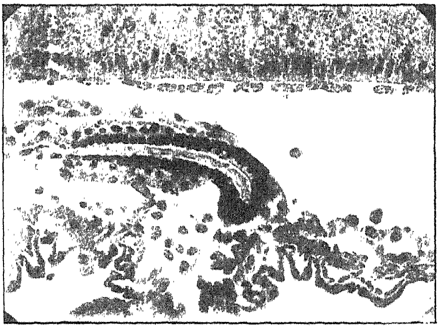


6

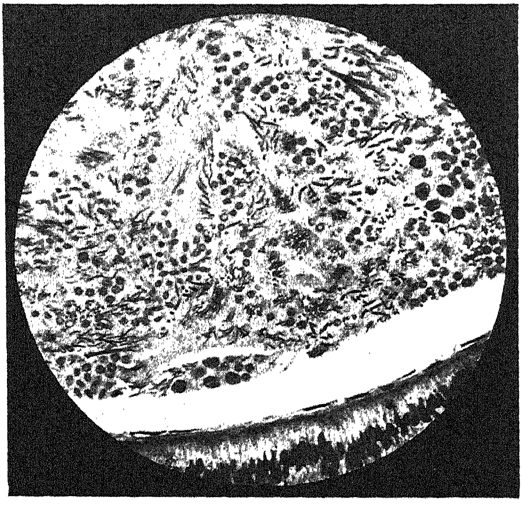


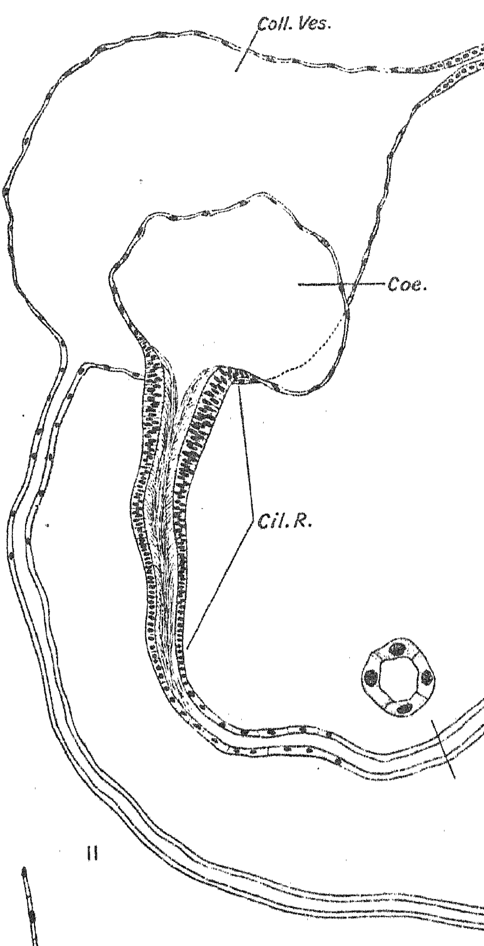


4

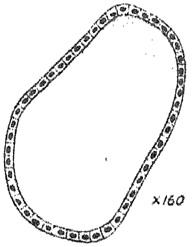


12

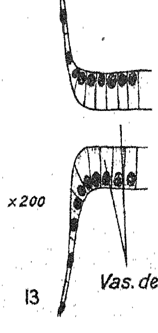




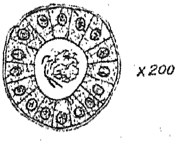
11



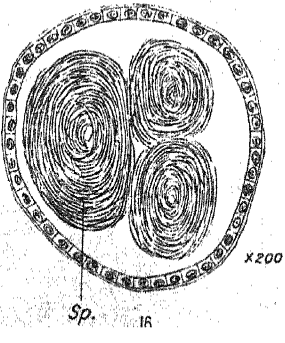
10



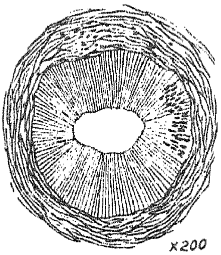
13



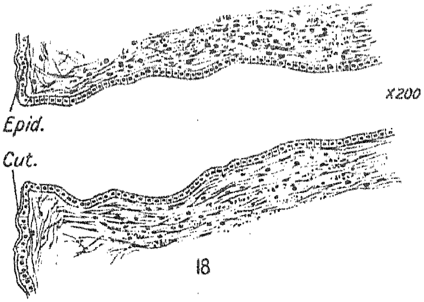
15



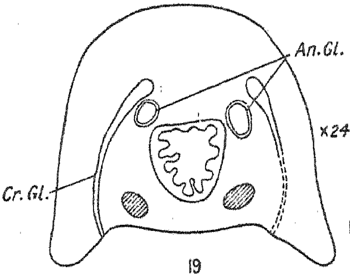
16



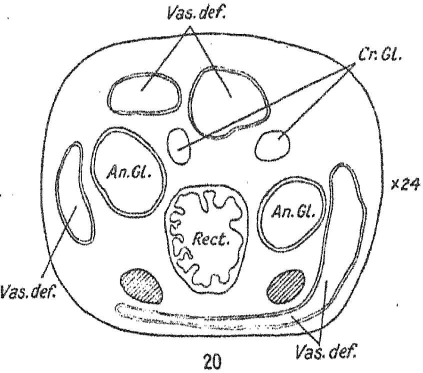
17



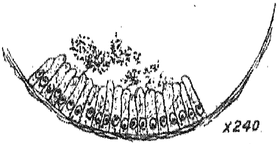
18



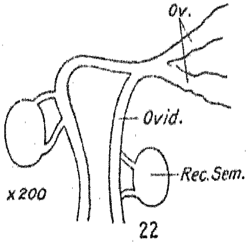
19



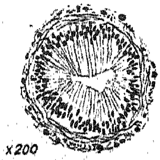
20



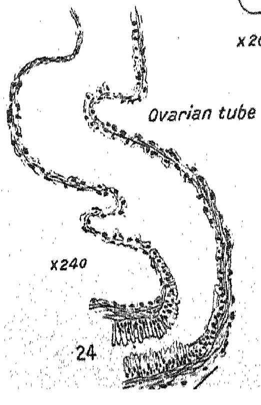
21



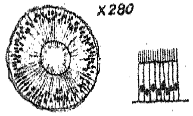
22



23



24



25

20. Fauna of Western Australia.—III. Further Contributions to the Study of the Onychophora. The Anatomy and Systematic Position of West Australian *Peripatoides*, with an account of certain histological details of general importance in the study of Peripatus. By Wm. J. Dakin, D.Sc., F.Z.S., F.L.S., Professor of Biology, University of Western Australia.

[Received March 16, 1920: Read May 11, 1920.]

(Plates I.-V.*)

INTRODUCTION.

There are yet many details of interest in the structure of Peripatus which remain problematic. The histology of the eye and the structure of the tracheæ may be cited as examples; whilst even the presence of cilia, an unusual character for an arthropod, has been doubted by some histologists.

In addition to general features, such as the above, there is always the consideration that the anatomy of the different species of Peripatus should be thoroughly well known, especially as in many places there is a tendency for the advance of civilisation and closer settlement to drive this somewhat rare animal to extinction. It has been comparatively easy in Western Australia for the author to procure specimens of this interesting group of arthropods and the facilities for examining specimens being so to speak on the spot, there seemed a likelihood that a close study would reveal something new regarding the West Australian species at least. Further support was lent to this view by reason of the fact that one West Australian species, the first to be discovered, had only been collected once many years ago, and was very briefly and quite insufficiently described. Practically no details of the anatomy were known.

In all, three species of Peripatus—or, perhaps more correctly, *Peripatoides*—have been recorded from Western Australia, namely:—

1. *Peripatus leuckarti*, var. *occidentalis* Fletcher, syn. *Peripatoides occidentalis* Dendy.
2. *Peripatoides gilesii* Spencer.
3. *Peripatoides woodwardi* Bouvier.

Of these three, *Peripatoides occidentalis* was the first to be collected. It was discovered about 160 miles south of Perth, at

---

* For explanation of the Plates, see p. 388.

Bridgetown, by a Mr. Lea and named by Fletcher (Proc. Linn. Soc. N.S.W. 1895 (2) x.). Twelve years later, Peripatus was found in another locality much farther north, in the hills at Armadale, only about 18 miles from Perth. Specimens of these collected by Mr. H. M. Giles were sent to Professor Baldwin Spencer. He found them to belong to a new species, and in a short paper, published (**12**) in 1909, named it *P. gilesii* after the collector. Specimens of the supposed third species had been collected four years before this, *i.e.*, in 1905, by a German Expedition (The Hamburg Exped. of Michaelsen and Hartmeyer). They were also collected near Perth and in the hills. These specimens were sent to Bouvier, who wrote a detailed description of the anatomy and discussed the relationships of the species to other known Australian forms. Bouvier's paper (**3**) appeared in 1909, the same year in which Spencer's description of *P. gilesii* was published. The supposed occurrence of two species in the same district and the fact that both descriptions appeared in the same year aroused the curiosity of the present author, and the result of his investigations (see Proc. Zool. Soc. London, June 1914) confirmed his suspicions. *Peripatoides woodwardi* and *Peripatoides gilesii* turned out to be one and the same species, and since Spencer's description was published some months before Bouvier's paper, the name *P. gilesii* took precedence over *P. woodwardi*. The fullest account of the species is, however, to be found in the paper of Bouvier (**3**) under the name of *P. woodwardi*. Now, since the previous publication of the writer (Dakin, Proc. Zool. Soc. 1914), an exploration to the S.W. resulted in the collection of over 100 specimens of the Peripatus first made known from West Australia, *i.e.*, *Peripatoides occidentalis*. The consequence was that the entire question was reopened. About 100 specimens of *P. gilesii* were collected for the purpose of a detailed examination and comparison of both species, the northern and southern. The conclusion of this research was rather surprising. In all the peculiarities that marked the northern species (*P. gilesii*) the southern species agreed. The difference between the two forms was so slight that we could not regard them as more than varieties.

Thus we have reduced the number of species of *Peripatoides* in West Australia from three to one. The southern type must retain the name *Peripatoides occidentalis*—the northern form should be known as *Peripatoides occidentalis* var. *gilesii*. Further than this, however, a detailed investigation of the specimens has shown that Bouvier's description of the anatomy contains several inaccuracies, some of which are decidedly important from the point of view of comparisons. These inaccuracies are without doubt excusable, for the number of specimens at the disposal of Bouvier was small and the preservation could not have been all that was to be desired.

OCCURRENCE OF THE SPECIMENS OF PERIPATOIDES IN WEST AUSTRALIA.

It is noteworthy that all the specimens of Peripatus taken up to date have been found in the hills and at some little elevation away from the coastal plains. On the other hand they have not been found very far into the interior. They have been found in situations which, at least during the winter months, are somewhat damp but not excessively so. There is no doubt that Peripatus extends over a wide area in West Australia, but it is very difficult to map out this area, for collecting is not exactly an easy task and the animals have their usual eccentric local distribution within it. For example, the author went out on one occasion to a small valley in the hills where Peripatus was believed to occur. An entire morning was spent searching without signs of a specimen, and it was decided that after lunch a new spot should be tried further ahead—the next little valley, in fact. The next valley turned out, however, to be the one where we had imagined ourselves all the morning, and we soon found Peripatus there as on previous occasions. Here were two little valleys only ten minutes apart, with the same vegetation, the same amount of moisture, and presenting such a similar appearance that one had been mistaken for the other. Yet in the one we found many specimens of Peripatus, in the other, none.

Specimens have up to date been captured at the following places:—Lion Mill, Mundaring Weir, Armadale, Kelmscott, Kalamunda (all specimens found at these places were supposed to be *P. gilesii*), and at Jarrahdale and Bridgetown in the S.W. (*P. occidentalis*).

Most specimens have been obtained at Mundaring Weir, Armadale, and Jarrahdale. At the latter place 13 specimens were found under a small piece of branch about 1 foot square, and nearly 150 specimens were captured in three days. Very few indeed have been found under stones or under bark or fallen trees. The usual place is on the surface of the soil underneath a small or large piece of wood (a fallen branch or part of one). Here the ground is more or less damp and there is no grass. In the same situation white ants are by far the most ubiquitous creatures, with nests of true ants frequently lending variety. Large centipedes are often common, but not usually with Peripatus, which prefers, on the whole, the absence of ants, centipedes, and millipedes from its particular sheltering log.

In the summer no specimens have ever been found and this despite some very arduous work in the broiling sun. Peripatus is, however, extremely sensitive to drought, and before the dry season—November or December to April—it must find its way either below the surface of the ground or far into the crannies and cracks in fallen and decaying logs. As the breeding season coincides with the dry season it is impossible to study the embryology of West Australian Peripatus, unless specimens are kept alive under artificial conditions in the laboratory through the long summer.

The regions in the hills where Peripatus is found are baked dry in the summer, and the temperature rises frequently to 104° F. in the shade in these valleys. The hidden recesses where protection is sought must be somewhat moist, for on several occasions the mere carriage of specimens for a few hours in a cardboard box, with none or insufficient moist earth, has resulted in the death of the animals through drying up. This is all the more noteworthy, since half-a-dozen specimens will live for days in a small glass tube. When suddenly exposed to the light of day the animals remain motionless, but after a few minutes they may move quite actively to get out of the light. Slime is often ejected from the slime glands on touching the specimen with the forceps or the finger.

EXTERNAL CHARACTERS.

Colour and Pattern.

Both the varieties of *Peripatoides* occur in two rather different colours, brown, and dark olive-green, and the numbers of each are practically equal. Between these two shades there are specimens bearing various intermediate tints, and frequently the brown specimens are so marked with dark brown (almost black) that they have quite a variegated appearance.

Closer investigation with a dissecting binocular microscope brings out the fact that the entire surface of the animal's body is covered with small papillæ. The pigment in the brown specimens is arranged as follows: There is an almost uniform brown background from which arise the papillæ above mentioned. These papillæ are either brown (a little darker than the background) or jet black. Some of them, however, have a pale yellow area round the base. The arrangement of the papillæ is responsible for the dark patterns of the skin.

In a very dark brown specimen the effect is due to the background being much darker, the papillæ remain the same, and the pale yellow areas, as round the bases of certain black-tipped papillæ, are conspicuous. If the background is still darker—almost black—with a slight tinge of the brown in it, the effect of the black papillæ, the pale yellow areas round some of them, and the colour of the background is to produce the very dark olive-green shade of some of the specimens.

The ventral surface is more free from papillæ and the general background is an almost clear white. In the bright brown specimens, between the legs of each pair there are two patches where the background is a pale grey—a patch to either side of the middle line. On each patch there are minute black papillæ. Between each successive pair of legs the background is more or less tinged with pale orange brown and there are minute darker orange papillæ. Each ring here bears larger and more separated papillæ which are quite white. They seem to correspond to the white areas round papillæ of the dorsal surface.

In both varieties an extremely fine light median line runs the length of the dorsal surface. It may not appear so in all specimens at a first glance. This, however, is due to the fact that in the light brown specimens, where it seems clear, it runs down the middle of a narrow band somewhat paler in colour than the rest of the dorsal surface and rather free from papillæ. In the dark specimens, on the other hand, this narrow band is darker than the rest of the dorsal surface, and with the naked eye or low power may be all that is observed. A higher magnification will show that a very fine light line runs through it medially, as in the light-coloured specimens.

The longitudinal band of the dorsal surface referred to above is related to a slight depression, the fine white line being an extremely narrow groove. The narrow band was noted by Bouvier, but the fine median white line escaped his notice.

In both varieties there are always a number of clear white papillæ between the successive legs at about the ventral margin of the flanks. These correspond, however, to the large papillæ of the dorsal surface and have merely lost the black pigment—they are identical with the large clear papillæ of the ventral surface.

The skin is thrown into a number of folds or ridges, as is usual in Peripatus. There are about 14 of these between two similar points opposite two successive legs. The ridges are to be seen both dorsally and ventrally, but are not continuous round the entire circumference of the body, for they are interrupted in the middle of the dorsal surface by the longitudinal line. But for this, however, some are continuous. Others arise between these larger folds and do not run so far. Naturally those opposite the legs are not continuous on to the ventral surface. The folds are not all of the same width, but it can hardly be said that they are alternately wide and narrow in either variety. There is really very little difference.

ORAL PAPILLÆ.

The oral papillæ are to be found in their usual position—there is nothing of particular interest to add with regard to them.

On many occasions slime was shot out from the openings of slime glands on these oral papillæ when the specimens were touched. It was emitted in large quantities when the animals were dropped on to water containing a little formalin, and also when the specimens were narcotised with chloroform.

THE CEPHALIC REGION.

Bouvier (3) has described in considerable detail the rings or ridges of the integument at the bases of the antennæ and in the neighbourhood of the eyes. He recognises in certain Peripatus species what is termed an *ocular ring* of papillæ, with part of it differentiated to form a frontal organ. In others he states: "l'arceau oculaire s'attenue, puis disparait assez brusquement après avoir décrit un peu plus d'un demitour, mais à ce niveau ou même bien plus en dédans, l'arceau infra-oculaire prend une remarquable prédominance, forme parfois un organe frontal et se continue par l'arceau spiral." The northern variety (Bouvier's *Peripatoides woodwardi*) is supposed to be one of the forms most typical of this group of species.

Several specimens of both varieties have been examined, and, so far as can be made out, there is no difference greater than the variations met with in either variety, between the two forms.

THE LEGS.

The number of legs appears to be very definite in the West Australian *Peripatoides*, and no variations are to be recorded *amongst the individuals from any one area*. There is, however, a marked difference between the two varieties which inhabit the northern and southern areas respectively.

Bouvier stated that *Peripatoides gilesii* resembled *P. suteri* and differed from all the other Australian *Peripatoides* in the possession of 16 pairs of legs. At the same time it was stated to differ from *P. suteri* in only having three pedal papillæ, in which respect it agreed with other *Peripatoides*.

Fletcher diagnosed the southern variety, *P. occidentalis*, as possessing 15 pairs of walking-legs, but no further description was given. This is the difference between our two varieties, and it is most constant. All the specimens from Mundaring, Armadale, Kelmscott, etc., in the north, have 16 pairs of legs, whatever be their size or sex. All the southern specimens bear only 15 pairs of legs. All the legs are similar with the exception of the 4th and 5th pairs in both varieties, from which one may conclude perhaps that it is one of the posterior pairs that is missing in the southern type.

Each leg is marked by rings bearing papillæ, but near the apex on the ventral surface these papillæ have united to form spinous pads, the middle one of which is somewhat wider than the others. Now in the northern variety the 4th and 5th pairs of legs differ from the others in the fact that the proximal spinous pad is segmented, a small central segment being cut off from two larger lateral lobes. This central segment takes the form of a papilla upon which the duct of the excretory organ opens. They are accurately figured by Bouvier, who remarks that the urinary papillæ of the 4th and 5th legs are always independent of the neighbouring parts of the proximal spinous pad, whereas they are always adherent in *Peripatoides suteri* and sometimes in *P. orientalis* (*P. leuckartii*). We may now add that the condition described above holds good in every detail for the southern form too.

THE MANDIBLES.

The character of these structures has been used very considerably in systematic works, and consequently they have more than a little interest for us here.

Each mandible consists as usual of two blades. The outer blade presents a single large projection, but no small teeth. The inner blade is provided with a large principal tooth and a number of smaller accessory teeth. According to Spencer (**12**) there are four clearly marked and one minute accessory tooth, whilst Bouvier remarks that, as in *P. suteri*, *P. novæ zealandiæ*, and *P. occidentalis*, there are five accessory teeth. In the course of this present research the mandibles have been removed from a large number of specimens, and examined, with the result that whilst one can say that five accessory teeth are most common upon the inner blade, there may be six or even seven. In the latter case the extra teeth are very small. There is again no difference to be noted between the northern variety and the southern form previously known as *P. occidentalis*. There is never an accessory denticle at the base of the large tooth on the outer jaw blade.

EXTERNAL SEXUAL DIFFERENCES AND CRURAL PAPILLÆ.

There is no difference in the number of legs borne by the two sexes as in *Peripatus novæ-britanniæ*, although the two sexes are to be distinguished by other characters associated with these appendages, *i. e.*, the crural papillæ. The female aperture is larger than the male aperture, as noted by Bouvier, and both apertures are found between the bases of the legs of the last pair. Behind the aperture of the reproductive organ in the male, and consequently just posterior to the last pair of appendages, are two small openings which can be recognised by their slightly tumid, pigmentless lips. These are the apertures of the anal glands.

The Crural Papillæ are the most distinctive features of the male. Unfortunately there has been some confusion as to the number present, and these structures have been taken as of considerable systematic importance. Bouvier (**3**) gives the following table for three males in his collection (the species formerly known as *P. woodwardi* or *P. gilesii*):—

Legs		1.	2.	3.	4	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.
Sp. c.	Rt.	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	0
	Lft.	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0
Sp. d.	Rt.	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
	Lft.	1	1	1	0	1	1	1	1	1	1	1	1	0	1	0	0
Sp. t.	Rt.	1	1	1	0	0	1	1	1	1	1	0	0	0	0	0	0
	Lft.	0	1	1	0	0	1	1	1	1	1	1	0	0	0	0	0

It will be noticed that there is a very large amount of variation. Bouvier found, however, that in many cases the papillæ could be discovered by a study of the anatomy. He concluded that there was reason to believe that *Peripatoides woodwardi* possessed crural papillæ for all the legs with perhaps the exception of the *last two pairs*, although further investigation might show them to exist there too.

In making a comparison with other Australian species of *Peripatoides*, Bouvier states (relying on Fletcher's description of *P. occidentalis* (7)) that our northern variety *differs from all other Australian forms in the possession of crural papillæ on the 1st pair of legs*. In fact, this is stated to distinguish *P. woodwardi* from *all* other known species of Peripatus. This statement renders an examination of the southern variety particularly interesting.

Let us first take Bouvier's northern type. We have found that the mere presence or absence of crural papillæ when examined externally means almost nothing. Sections show *always* that the papillæ are present on certain legs but that they may be either invaginated (see Pl. III. fig. 4, Crur. pap.) or protruded. Every specimen examined has had different crural papillæ protruded. It may either depend upon the fixative or the animal may protrude certain papillæ at definite times. The preserved specimens would then indicate the condition at the time of fixation.

The fact remains, however, that crural glands are present in the male in every leg (Pl. I. fig. 3, Cr.Gl.), and papillæ are to be found on all of them too. This is a correction to Bouvier's otherwise excellent description, for he is not certain of their presence on the penultimate pair. They are rudimentary on this pair, corresponding to the condition of the crural gland, which is very small in these legs (see Pl. I. fig. 3). The papilla is well developed on the last legs, and its place is marked even when withdrawn by a minute aperture with raised lips.

It is striking to find that the above description will answer exactly for the southern form (*P. occidentalis*). Males have been obtained with almost all the appendages showing protruded crural papillæ. Sections indicate the presence of crural glands and crural papillæ exactly as they are found in the Mundaring specimens. We must emphasise in this connection the necessity for the external examination of many specimens before one can state how many crural papillæ are present. Thus we now have two varieties (of one species) which are characterised by the possession of crural papillæ on the 1st pair of limbs.*

---

* The above puts out of court Fletcher's description of *P. occidentalis* in which he states that the males have white papillæ on most of the legs, *but not on those of the 1st pair*.

INTERNAL ANATOMY.

ALIMENTARY CANAL, ETC.

The alimentary canal presents nothing of exceptional importance in the way of differences from the conditions observed in other species of Peripatus. The jaws have already been described. A few words are necessary with regard to the muscles attached to them. It is frequently stated that the muscles of the mandibles are the only striped muscles in Peripatus. A careful examination of all the muscles in the West Australian *Peripatoides* has been made, but so far as transverse striation is concerned no differences can be made out between any of them. No muscles bear cross-stripes, all appear smooth.

SALIVARY GLANDS.

Two well-developed salivary glands are present, opening by a common duct ventrally into the mouth. The common median duct is very short (see Pl. I. fig. 1) and gives rise almost at once to two narrow tubes which run out at right angles to the long axis of the body and then bend suddenly backwards when the lateral body-wall is reached. This portion (Pl. I. fig. 1, Sal.G.d.) is non-glandular, and the walls consist of compact cubical cells. A marked change takes place when the ducts bend abruptly backwards to run in the lateral compartments in close proximity to the nerve-cord; the ducts pass here into the glandular region (Pl. I. fig. 1, Sal.Gl.) of the salivary gland. The cells of this part are often much vacuolated, and the nuclei are pushed to the bases of the cells, where they lie in close proximity to a thin muscle and connective-tissue sheath (see Pl. II. fig. 5).

The length of the salivary glands is such that they extend back to somewhere about the 7th or 8th pair of legs—that is to say, just beyond the middle of the body.

THE TRACHEÆ.

The respiratory organs of Peripatus have always been regarded as of special note in view of the interesting relationships of the Onychophora. It is somewhat surprising, then, to find that even to-day there is some doubt as to whether a spiral fibre is present in the tracheal vessels. Other points are also uncertain.

The respiratory organs, as is well known, consist of tracheæ. These are very delicate and of minute diameter. In the West Australian *Peripatoides* they could only be made out with difficulty in preserved specimens, although more easily in sections. They are, however, exceedingly clear when freshly killed specimens are dissected under water and examined with a Zeiss binocular dissecting microscope. Ample material has rendered this mode of examination possible.

Distribution of Tracheæ.—As is well known, the tracheæ of

Peripatus arise in bunches from the bottom of little epidermal pockets which may be termed stigmata or tracheal pits. For a varying distance the delicate tracheal tubes run in a bundle all more or less parallel to each other and without branching; gradually, however, the tracheæ separate off in large or small packets from the main bundle and radiate in different directions. The tracheæ of these bundles in their turn gradually separate until they run alone. As a consequence of this arrangement and the fact that only the larger main bundles are readily visible even when filled with air, each tracheal pit appears to give rise to a little irregular rosette or star of tracheæ. That is to say, this is the appearance when the inner surface of the body-wall is examined. The arrangement is indicated in the illustration (Pl. II. fig. 6).

The tracheal pits are arranged somewhat irregularly, but mainly in the manner indicated by Balfour in 1883 in *Peripatus capensis*. There are two irregular rows dorso-laterally on each side, that is in the quadrants between the heart (Pl. II. fig. 6, Ht.) (mid-dorsal line) and each longitudinal nerve (Pl. II. fig. 6, N.C.). The more ventral series on each side appears to comprise the larger bundles. On the ventral surface there are also four longitudinal series of tracheal pits, two to each side of the mid-ventral line (only two series, those to the left of the mid-ventral line, are shown in fig. 6). The row next to the longitudinal nerve on each side appears to comprise the larger bundles. It is difficult to say how many tracheal pits there are to a segment, for the number appears to vary, and the smallest ones are not easily seen. No attempt has been made to determine the full number. Gaffron (**8**) states that there are about 75 per segment in *Peripatus edwardsi*. We have counted over 32 without trouble in segments of our *Peripatoides*.

There are some very large tracheal bundles in the head, supplying the large nerve ganglia. Some of the largest of these arise ventrally, and there seems to be a series of tracheal pits surrounding the mouth-opening. Just behind the mouth there is a large pit in the mid-ventral line. There are also large pits ventrally placed and in the median line in front of the mouth. Other large pits occur to the sides of the oral aperture.

Branching of the Tracheæ.—A great deal of doubt has been expressed as to the course of the tracheæ in Peripatus. Thus, in Balfour's treatise on the Anatomy and Development of *P. capensis* (**1**), the following statement occurs: "Moseley states that the tracheæ branch, but only exceptionally." Balfour stated that the tracheæ were "extremely minute, unbranched (so far as I could follow them) tubes." Sedgwick, in his article in the Cambridge Natural History (**10**), states that the tracheæ "appear to branch but only exceptionally."

Now the *main* trunks do not branch in the West Australian *Peripatoides*, but if a piece of alimentary canal-wall in the fresh state is mounted in salt solution and examined with

$\frac{1}{12}$ oil-immersion lens, branched tracheæ can easily be found (see Pl. II. figs. 7 & 8).

The nerve-cords, ganglia, alimentary canal, and in fact all the organs are well supplied with tracheæ and branching is easily discovered. But it is only when an oil-immersion lens is applied to practically living tissues that the full extent of the tracheal system becomes apparent. Pl. II. fig. 8 shows more distinctly the manner of division of the tracheal vessels.

Pl. II. fig. 7 is but a very small area of the alimentary canal-wall indicating the course taken by the branching tracheal vessels there. Attempts to follow out with certainty the fine terminations of the branched tracheæ have so far met with little success. They simply end, but whether the end has been seen or whether still finer capillary tubes continue and penetrate cells is unknown.

The Structure of the Tracheæ.—Typical insect tracheæ are elastic structures lined by an extremely delicate chitin layer which is strengthened by a spiral fibre. The spiral fibre is said to be absent from the fine capillary twigs. In large insect tracheæ the spiral thickening is easily observed with a moderately low power of the microscope. The largest tracheæ of Peripatus are, however, of minute dimensions, and it is not surprising therefore that uncertainty should have arisen as to whether they presented the spiral so characteristic of other tracheate arthropods. Balfour noticed something and was led to state that the tracheæ exhibited a faint transverse striation which he took to be indicative of a spiral fibre. No one seems to have gone beyond this since, and Sedgwick (**10**) in 1910 restated it in the description: "The tracheæ are minute tubes exhibiting a faint transverse striation which is probably the indication of a spiral fibre." Gaffron (**8**) remarks that it is questionable whether a spiral fibre exists, the only indication being some fine cross striping seen only with high powers.

This question has been solved, like certain others, through the application of the oil-immersion lens to fresh material mounted in salt solution. There is now no doubt but that the delicate tracheæ of *Peripatoides* are strengthened by an excessively minute but perfect spiral fibre (Pl. II. fig. 9).

THE CRURAL GLANDS.

Reference has already been made to the crural glands in the section dealing with the external characters.

They are particularly well developed in the males, where a pair can be found for every pair of legs. With the exception of the glands of the first and last pairs of legs, which are highly modified in both the West Australian forms, the crural glands are entirely contained in the legs. The external aperture is very distinct. It is situated distally to the nephridial aperture on the ventral surface of all the legs except the 4th and 5th, where the excretory opening is found near the end of the appendage. The extremity of the gland-duct which opens to the exterior is provided with a swollen circular lip which forms the crural papilla. The surrounding epidermis is retractile and may be invaginated to form a little *Crural Pit.* The crural papilla is then quite invisible from the exterior, but this is merely a temporary condition, and consequently there is no point in counting visible crural papillæ in these animals unless the count is checked by sections. With the exception of the last pair of glands, opening on the last pair of appendages, the aperture of the gland leads to a narrow duct bounded by small cubical cells. This duct runs upwards to open into a large vesicle which extends distally and occupies quite a large extent of the leg-cavity. The vesicle itself, *i.e.*, the crural gland proper (see Pl. IV. fig. 10) is lined by a layer of small and compact cubical epithelial cells with large nuclei centrally placed. The glands are usually readily distinguished by reason of the contents, which in sections stained with hæmatoxylin and eosin appear bright pink. Still more characteristic is the fact that the contents are perfectly homogeneous and *non-granular.*

The first pair of Crural Glands differs considerably from all the rest. The duct opens in the same manner as in the succeeding glands but instead of leading to a sac in the leg it passes into the lateral cavity of the body and opens into an elongated sac which runs almost the entire length of the animal (see Pl. I. fig. 3, Cr.Gl.'). This tubular gland can be easily picked out in transverse sections, for it is always cut transversely and lies not far from the lateral nerve-cord and below the salivary gland in sections where this is also present. The structure of its wall is quite characteristic.

These extraordinary crural glands of the first legs were discovered in the West Australian *Peripatoides* from the hills near Perth by Bouvier. They are noted in his monograph as peculiar to the species. It is important, therefore, to note that the same feature is present in the southern variety—in short, this character is peculiar to both West Australian varieties of *Peripatoides.*

The Crural Glands of the penultimate legs are extremely minute. The duct is short and leads into a very small vesicle. Bouvier was uncertain as to whether crural glands existed here at all. He was unable to find them in his specimens.

The Crural Glands of the last pair of legs are very different from all the others. The ducts pass direct from the legs into the central body-cavity, where they lead into two somewhat wide tubes which run forwards entangled in the coils of the gonoducts (see Pl. I. fig. 3, Cr.Gl.").

Crural glands and crural papillæ are features of the male sex, but in Willey's account of the Anatomy and Development of *Peripatus novæ-britanniæ* (**13**) the following reference occurs to crural glands in the female: "Wherever they occur (crural glands) they are found only in the male except in *P. capensis*, where they are said to occur in the female also (Sheldon).

Without denying their occasional existence in the female *P. capensis*, I may say that I have failed to find them present, and I doubt, on *à priori* grounds, if they normally occur in the female."

In the paper (**11**) to which Willey refers the following statement is made: "I have examined several legs of *P. capensis*, both of males and females, and have found a crural gland in every one except the first pair of legs."

A careful search through sections of female *Peripatoides* of Western Australia has shown that crural glands *do* occasionally occur in the female. They are not always present, however, and when found there is no regularity as to the legs containing them. In any case they are not highly developed, although they have the same vesicle with the same pink-staining homogeneous contents found in the male.

THE NEPHRIDIA.

A very careful study of the nephridia of Western Australian *Peripatoides* has been made, and well-preserved sections have elucidated many points. It will be perhaps desirable to describe their structure in detail, especially since some features, the presence of cilia for example, are now made known for the first time. Mention of cilia occurs in all general descriptions of Peripatus, but only to the effect that they are found in the generative ducts. The cilia discovered in the nephridia of *Peripatoides* are remarkably well developed and of great length, reminding one more of flagella.

The nephridia, with the exception of those of the 4th and 5th pairs of legs, open on the ventral surface at the junction of each leg and the body. Those of the 4th and 5th pairs of legs are quite different from the others. They open on a special papilla situated on the ventral surface of the respective legs (see Pl. I. fig. 2, Neph.'). It is rather striking that with variations in the anatomy of the Onychophora, and in particular with considerable variations in the number of legs, there should be such a constancy in regard to the position of these special nephridia. They are of almost exactly the same form in the West Australian *Peripatoides* as in *Peripatus capensis*, and similar enlarged nephridia occur in other species.

Nephridia are found in all the pairs of legs without exception in the West Australian *Peripatoides*.

Structure of a typical Nephridium.—The aperture, which, except in the case of the 4th and 5th nephridia, is unmarked by any papilla, appears as a little crevice in the epidermis. This leads into a short tube of minute diameter. This duct passes upwards into the lateral compartment of the body and opens into a thin-walled collecting vesicle (Pl. IV. fig. 11, Coll. Ves.). The cells of the duct are small, cubical, or somewhat flattened, but the vesicle is lined by a very delicate squamous epithelium of large cells, the nuclei appearing distinctly some distance apart. The vesicle might easily be mistaken for a split in sections were it not for its constant presence and the ducts opening into it. Following the vesicle the nephridium is divisible into two marked sections, a tubular portion and a terminal chamber. The tube describes a rough circle and then turns abruptly on itself, so that its termination is close to the vesicle referred to above (see Pl. IV. fig. 11).

The terminal chamber (Pl. IV. fig. 11, Ce.) is now well known, although missed by the first investigators, who believed that the nephridia opened into the lateral compartment of the body. The chamber lies partly above and partly posterior to the collecting vesicle referred to above.

The first portion of the nephridial tube internal to the collecting vesicle is lined by a very delicate and characteristic epithelium of large flat cells. As a consequence of the size of the cells relative to the diameter of the duct it is possible to have transverse sections with only two or three nuclei showing (see Pl. IV. fig. 11). The greater part of the nephridium between the terminal chamber and the collecting vesicle is built in this way. The section, however, which actually opens into the terminal chamber is very different. The wall of the nephridium becomes thicker and far less delicate and is formed of a compact layer of columnar epithelial cells (see Pl. IV. fig. 11, Cil.R.). These cells are so crowded and the nuclei stain so distinctly that most previous workers have noted the peculiarity. In fact this change in the character of the cells has been taken as indicating the passage from the ectodermal part of the nephridium to the mesodermal portion (see Glen, Q. J. M. S. 1918, vol. lxiii.).

Now it is the cells of this section of the nephridium which bear the cilia (Pls. III.-IV. figs. 11 & 12). These are so long that after projecting from the cell they extend along the lumen of the duct for a relatively considerable distance. It is extraordinary that in many figures showing the structure of the nephridia of Peripatus details of the histology are given at a high magnification, yet no indication of cilia is presented.

Bundles of long cilia are very characteristic of renal cells, although at the same time they are in the highest degree peculiar for the arthropoda. The Annelid resemblances of *Peripatus* are certainly heightened as a result of the examination of well-preserved sections through the ciliated ducts of these nephridia*.

---

* Since writing the above I have been enabled to examine a copy of Gaffron's famous paper (**8**) on the Anatomy and Histology of Peripatus, in which the first mention of the presence of cilia in this animal—in the Receptacula seminis—was made. Looking through his description of the nephridia I found to my surprise the following lines referring to the region where the duct opens into the cœlomic vesicle. It must be remembered that the vesicle was unknown at the time, and its remains were supposed to be a funnel-like nephrostome opening into the body-cavity. "Er besitzt wie der Trichter selbst, kleinzelliges, im Leben *wahrscheinlich wimperndes Epithel* . . . ." Gaffron never indicates that he found cilia here nor are any shown in his illustrations of this region. We must conclude that the remark was merely a conjecture, probably suggested by the apparent resemblance to the open nephrostome of an annelid. It is curious, however, that his successors who have studied the nephridia have not commented on this. Either the cilia are only found in the West Australian *Peripatoides* or else my preparations must be particularly favourable ones.

The Nephridia of the 4th and 5th pairs of legs (Pl. I. fig. 2, Neph.'). These nephridia differ from the others firstly in the increased length of the tube between the distal collecting vesicle and the opening on the leg. This is due to the fact that the renal aperture is situated near the extremity of the appendage. The vesicle presents the same structure as before. From the collecting vesicle a long, tubular portion extends posteriorly within the lateral compartment of the body. This section presents the same type of wall as the corresponding section of the other nephridia. Having reached somewhere about the second succeeding pair of legs the tube turns on itself and runs forward, the two limbs being in close contact. The wall still presents the large flattened cells. This section passes into the ciliated duct, which is particularly well marked in these nephridia, and opens into the cœlomic chamber, which lies close to the distal collecting vesicle.

THE REPRODUCTIVE ORGANS.

A somewhat detailed description of the reproductive organs of the West Australian *Peripatoides* is rendered necessary owing to the fact that Bouvier's specimens of the northern variety were not sufficient to allow of a complete and accurate account of the anatomy. This applies in particular to the female, in which connection Bouvier states (**3**) "L'appareil génital femelle ne présente rien de particulier, si *ce n'est l'atrophie complète, ou à peu près complète, des receptacles séminaux.*" The receptaculum seminis is, however, well developed. The explanation of the mistake probably lies entirely in the state of preservation of the few specimens available. We have had the good fortune to obtain many specimens and to preserve them in many ways.

The Male Reproductive Organs consist first of the two testes, which lie fairly far forwards entangled amongst the diverticula of the slime glands (see Pl. I. fig. 3, Tes.) and dorsal or lateral to the alimentary canal. These organs are tubular and from the wall cells are cut off which are apparently the spermatocytes. *These do not develop into spermatozoa in the testes. Apparently the development of spermatozoa takes place in the vesicula seminalis* (see Photomicrograph, Pl. III. fig. 14).

This feature is to my mind rather interesting; yet it is one which is never mentioned in text-books. It was naturally thought at first to be quite a new discovery. As a matter of fact it was seen by Gaffron many years ago and figured in his work (**8**). Gaffron was struck also by the resemblance to the conditions in the earthworm and actually writes: "Etwas æhnliches findet sich bekanntlich beim Regenwurm, wo ja auch die eigentlichen Hoden den 'Samenblasen' gegenüber sehr zurücktreten und die Weiterentwicklung der Spermatozoen in letzteren stattfindet."

Each testis opens into a seminal vesicle (Pl. I. fig. 3, S.V.), one usually lying somewhat in front of the other owing to the crowded condition of the body-cavity. It is difficult to separate the delicate ducts in preserved and consequently hardened specimens. The seminal vesicle may, however, attain such a size at a certain season of the year (September-October) as to fill up most of the body-cavity where it occurs. This is well shown in the illustration Pl. III. fig. 4, which is a photomicrograph of a transverse section passing through such a seminal vesicle. The wall of the seminal vesicle is rather delicate, being formed of somewhat flattened epithelial cells (Pl. IV. fig. 13). The vas deferens leaves the seminal vesicle at the opposite side from the entrance of the testis or testis duct. (It is impossible to divide that portion of the reproductive organs beyond the seminal vesicle into regions.)

The first portion of the vas deferens following the seminal vesicle is lined by almost cubical cells (Pl. IV. figs. 13, 15). This leads imperceptibly into a section (by far the longest) the wall of which is of flattened cells, the epithelial layer being, however, supported by a layer of longitudinal and circular muscle fibres. This section of the vas deferens coils about, entangled with its fellow of the opposite side and also with the terminal portions of the accessory reproductive glands.

What we may term the vas deferens of the right side continues its course to the left of the alimentary canal right away on towards the posterior extremity of the animal (see Pl. I. fig. 3, Vas.def.r.). Just in front of the male opening it dives under everything, even the two nerve-cords, and, reaching the right side, it continues its way anteriorly again.

This extraordinary difference from the course of the other vas deferens (Pl. I. fig. 3, Vas.def.l.) is always met with. It was indicated by Bouvier, but his drawing is not quite accurate.

Eventually, somewhere about the 4th or 5th leg from the posterior extremity, both vasa deferentia join up to form a very wide terminal unpaired tube. The first portion of this wide duct has thin walls, the epithelium consisting of flattened cells (Pl. IV. fig. 16). As the reproductive aperture is reached the walls become thicker (Pl. V. fig. 17) owing to a gradual development of transverse and longitudinal muscles. The terminal portion (Pl. V. fig. 18) is very muscular, the walls being quite thick. It is probably extrusible. This last section turns over to the right side of the alimentary canal and passing underneath the right nerve-cord reaches its opening to the exterior (see Pl. I. fig. 3).

As Bouvier pointed out, the vast chamber formed by the commencement of the unpaired duct is usually filled with a mass of spermatozoa, the whole taking the form of a convoluted cord (Pl. IV. fig. 16, Sp.). There is no sign of any chitinous envelope. It will be seen that the unpaired section of the reproductive ducts formed by the union of the two vasa deferentia is the region for the storage of spermatozoa and their massing into spermatophores—not the so-called seminal vesicle, where spermatogenesis takes place.

From the fact that sperms are found throughout the ducts of the female I have no doubt that females are impregnated through the vaginal aperture.

Accessory Ducts, etc.—The crural glands of the last legs of the male are modified as already pointed out. The minute duct, which opens in the usual place, runs into the central body-cavity and enlarges to form a thin-walled vesicle which runs forwards as far as the antepenultimate leg or thereabouts. It walls and contents (see Pl. IV. fig. 10) are similar to those of the normal crural glands of the anterior limbs.

Two other accessory glands, the anal glands, open in close proximity to the male reproductive opening, and slightly posterior to it. From each opening a narrow duct passes laterally under the nerve-cord and then turns dorsally and inwards and forwards, gradually widening until a rather wide sac is produced (Pl. I. fig. 3, An.Gl.).

These glandular sacs are rather prominent in transverse sections near the posterior end of the animal (Pl. V. figs. 19 and 20, An.Gl.), and are easily picked out by reason of the intensely vacuolated cells which form their walls. The contents, too, are very granular and deeply staining (see Pl. V. fig. 21).

The Reproductive Organs of the Female.—The ovaries of the West Australian *Peripatoides* agree with those of the other Australian forms and with the Cape and New Britain species in having thin walls, so that the developing eggs come to hang freely in the central division of the body-cavity (Pl. I. fig. 2, Ov.). From each organ an oviduct (Ovid., Pl. V. fig. 22) leads forwards for a short distance to open into a large and fully developed receptaculum seminis by two ducts (Pls. I., V. figs. 2, 22, Rec.Sem.). It is true that the receptaculum may reach a much larger size in September–November, but it is none the less a well-defined permanent structure at all times.

The oviducts, which open into the two ovaries, unite for an extremely short distance at their origin and then separate again (Pl. V. fig. 22). Their course is then amidst the convolutions of the slime-glands for a short distance to the point where each communicates with a receptaculum seminis. This first section of the oviduct is characterised by somewhat thick walls, the epithelial cells are deep and crowded together, the lumen of the duct usually appears restricted (see Pl. V. fig. 23).

As Willey noted in the case of *Peripatus novæ-britanniæ*, the walls of this first section of the oviduct differ from those of the rest of the genital duct. Willey (**13**) termed this portion the *infundibulum*, and remarked that the striking contrast between the infundibula and the ovarian tubes seen in *P. novæ-britanniæ* has not been remarked in other species.

The infundibula of the West Australian *Peripatoides* do not differ materially from those of *P. novæ-britanniæ*. So far, however, as the ovarian tubes are concerned, I have been able to distinguish peritoneal investment, tunica muscularis, and germinal epithelium, and the thickness of the wall increases as we pass to the infundibulum (Pl. V. fig. 24). I should be inclined, on the whole, to doubt the possibility of the ovarian tubes not being strictly homologous structures throughout the genus—a suggestion of Willey's.

The receptacula seminis (Pl. V. fig. 22, Rec.Sem.) are two thin-walled bags, each of which communicates with the infundibulum of its side by two short ducts. The same condition is met with in other species of Peripatus where the receptaculum is present.

The preparations which I have at my disposal show that cilia are present in the tubes connecting the infundibulum with the receptaculum (see Pl. V. fig. 25). This is the position in which cilia were first discovered in Peripatus by Gaffron (**8**). It must be noted that these cilia are much shorter and less distinct than those described earlier in this paper as occurring in the nephridia.

The two uteri do not differ essentially in histological structure from the infundibula. They possess a well-developed musculature—transverse and longitudinal fibres surrounding the epithelial wall. These uteri pass forwards for a short distance and then return, usually one to each side of the alimentary canal (Pl. I. fig. 2, Ut.). They meet posteriorly quite near the external aperture, and a median and very short vagina (Pl. I. fig. 2, Vag.) leads to the exterior. During the summer months each uterus presents the appearance of a string of sausages. This is due to the chain of developing eggs or embryos contained within it. The eggs are of very large size indeed, and the uterus is swollen considerably round each and constricted between them. The West Australian examples of *Peripatoides* bring their reproductive organs to maturity during the winter, which is the only period of feeding and activity in general. Fecundation probably takes place about August to October. The species is viviparous. [For further reference see notes on Spermatogenesis and Reproduction in a following paper.]

SUMMARY OF CHARACTERS DIAGNOSTIC OF THE WEST AUSTRALIAN *PERIPATOIDES*.

There are two West Australian varieties of Peripatus—subgen. *Peripatoides*. They agree in external characters and in anatomy, with the exception that whilst the northern form possesses *constantly* 16 pairs of legs, the southern variety has only 15 pairs. It is not considered advisable to separate these two forms as distinct species. They can only be considered varieties. The first to be discovered and named was the southern variety, which was termed *Peripatus leuckarti* Sang., var. *occidentalis*, by Fletcher in 1895.

Since that date, however, this western form has been raised to specific rank by Dendy (5), and is now recorded as *Peripatoides occidentalis*. The rediscovery of the typical form and the demonstration that its anatomy is almost identical with that of the other form which Bouvier recognised as quite distinct from all other Australian *Peripatoides* endorses Dendy's action. The northern variety was termed *P. woodwardi* by Bouvier, but we have shown (4) that this name lacks priority, the name *P. gilesii* having been previously given by Baldwin Spencer. The position is, therefore, that the only West Australian species of *Peripatoides* is *Peripatoides occidentalis*, the southern form being the original one named, the northern is thus to be known in future as *P. occidentalis* var. *gilesii*.

Previous diagnoses of *P. occidentalis* are to a large extent incorrect.

The Diagnosis of the Species is as follows:—

(1) Specimens fall into two colour series, in one of which dark green-black predominates, in the other a brown-red. (2) The legs number 16 pairs in the var. *gilesii*, 15 in the typical form. (3) The third pedal ring (or spinous pad) is usually slightly narrower than the first, and the intermediate ring a little larger than in the other *Peripatoides*; the rudiments of the 4th ring are practically invisible. (4) There are no accessory teeth on the outer blade of the mandible, and 5 or 3 on the inner blade. (5) The urinary papillæ of the 4th and 5th legs are each on a separate segment of the first pedal ring. (6) The crural papillæ are present on all the legs of the male, but may not be obvious owing to retraction. (7) Crural glands are present opening on all the legs; those of the 1st pair are very long and extend almost the entire length of the body in the lateral compartments. Those of the last pair of legs are also long and run forwards entangled with the reproductive ducts in the central body-cavity. All the other crural glands are contained in the legs. Those of the pair of legs preceding the last are very small. (8) The male reproductive organs may extend forwards as far as the 6th or 7th pair of legs from the posterior extremity. The two vasa deferentia after leaving the vesiculæ seminales in which spermatogenesis takes place run a tangled course. That of the right side runs almost to the extreme posterior end and to the left side of the body, it then curves under both nerve-cords and runs forward on the right side to meet its fellow and form an unpaired duct at about the level of the 4th or 5th pair of legs from the posterior end. The proximal portion of this duct is very wide and very thin-walled and forms a reservoir where spermatozoa accumulate in tangled "cordons." It passes gradually into a short muscular ejaculatory duct. (9) The ovaries are dorsal in position and extend forwards from near the posterior end, occupying the hinder third of the body at the breeding-season. The walls of the ovaries are thin, and the eggs when ripe appear

in consequence to lie freely in the central cavity of the body—in reality the ovary-wall projects in the form of very delicate follicles. (10) Receptacula seminis are present, each communicating with the oviduct of its side by two ducts which are ciliated.

AFFINITIES OF THE WEST AUSTRALIAN PERIPATOIDES.

Bouvier discusses at some length the affinities of his *Peripatoides woodwardi*. His account requires bringing up to date owing to the corrections necessary by reason, first, of the increased knowledge of this northern variety, and, second, owing to the information now brought forward regarding the anatomy of the southern form known to Bouvier as a distinct species. According to Bouvier the West Australian Peripatus is remarkable for its multiple affinities. It is supposed to resemble *P. suteri* of New Zealand by the presence of 16 pairs of legs and by the absence of an accessory tooth on the outer blade of the mandible. At the same time it is distinguished from this species by most other characters and resembles *P. leuckartii** in the following:—1, alternation of tegumentary folds; 2, reduction of the pedal papillæ to three; 3, the relative dimensions of the rings of the soles; 4, the multiplicity of the crural glands; 5, the analogy of the anal glands; 6, a certain resemblance in the unpaired portion of the male gonoduct.

It is, however, different from all other species in the possession of crural glands on the first legs—glands of enormous length. It is supposed to be unique in the constant presence of 16 pairs of legs with 3 papillæ. Its unpaired male duct is supposed to be really like no others. In short, it is supposed to present a mixture of primitive characters with others indicating a long evolution. These may be classified as follows:—

Primitive Characters.	*Advanced Characters.*
1. Crural glands opening on each leg.	1. No teeth on outer blade of mandible.
2. 16 pairs of legs.	2. Pedal papillæ reduced to three.
	3. Seminal receptacles atrophied.
	4. Character of male gonoduct.

I do not consider that we can lay much stress upon affinities which are only indicated by the presence of 16 versus 15 pairs of legs or the presence or absence of an accessory tooth on the outer mandible-blade. Surely some such change as this could have occurred as a mutation over and over again. In any case the West Australian species occurs in two forms, one with 16 and one with 15 pairs of legs, so that the resemblance to *P. suteri* does not hold good.

---

* *P. leuckartii* is taken as the correct name for the common Peripatus of the East, usually designated *P. orientalis* by Bouvier. For a discussion on the nomenclature of this species see Dendy (Q. J. M. S. vol. xlv. p. 388, and Zool. Anz. 1906, pp. 175–177).

As a matter of fact *Peripatoides occidentalis* approaches most closely *Peripatoides leuckartii*, and in addition to the resemblances noted by Bouvier we may add that receptacula seminales *are* present in both forms. The species is, however, very distinct from all other Peripatus species, and thus from all the other Australian species (which is not surprising seeing that the two Peripatus regions are separated by over two thousand miles, the greater part of which is country quite uninhabitable by Peripatus) in the presence of extraordinarily long crural glands opening on the first pair of legs. The northern variety is the only known Peripatus in Australia having 16 pairs of legs.

SUMMARY OF RESULTS OF GENERAL IMPORTANCE.

(*i. e.* probably applicable to most if not all species of Onychophora.)

I. The cells of a certain part of the so-called nephridium—that which opens into the terminal cœlomic vesicle—bear long and well-developed cilia. Thus cilia occur in the excretory ducts of Peripatus as well as in the reproductive organs.

II. Crural glands *do* sometimes occur in the female, but do not seem to possess any ducts.

III. The tracheæ of Peripatus possess a characteristic spiral supporting fibre.
(This has been a disputed question for many years.)

IV. The tracheæ of Peripatus, although running a separate course for some distance from the tracheal pit, eventually branch (see Pl. II. figs. 7 & 8).

V. Spermatogenesis does not take place in the testis but in the seminal vesicles. This discovery, made originally by Gaffron, seems to have been lost sight of in most descriptions of Peripatus.

LITERATURE CITED IN TEXT.

1. Balfour.—Anatomy and Development of *Peripatus capensis*. Q. J. M. S. 1883.
2. Bouvier.—Monographie des Onychophores. Ann. des Sci. Nat. (9) 2 & 5. Paris, 1905 & 1907.
3. Bouvier.—Onychophora. Die Fauna Süd-West Australiens, Bd. ii. Lief. 18. Jena, 1909.

4. Dakin.—The Onychophora of West Australia. Proc. Zool. Soc. London, 1914.

5. Dendy.—On the Oviparous Species of Onychophora. Q. J. M. S. vol. xlv. p. 388.

6. Dendy.—Zool. Anz. Bd. xxx. Nr. 6, 1906, pp. 175–177.

7. Fletcher.—On the Specific Identity of the Australian Peripatus, etc. Proc. Linn. Soc. N. S. W. 1895, vol. x.

8. Gaffron.—Zoolog. Beiträge (Schneider). Breslau, 1883.

9. Sedgwick.—Various papers on *Peripatus*. Reprinted in vol. iv. Studies from the Morphological Laboratory of the University of Cambridge. 1889.

10. Sedgwick.—Article on Onychophora in Cambridge Natural History.

11. Sheldon.—Anatomy of *Peripatus capensis*, etc. Q. J. M. S. vol. xxviii. 1888.

12. Baldwin Spencer.—Proc. Roy. Soc. Victoria, vol. xxi. (n. s.) pt. 2, 1909.

13. Willey.—Anatomy and Development of *P. novæ-britanniæ*. Zoological Results. Part I. 1898.

DESCRIPTION OF FIGURES.

Plates I.–V.

Peripatoides occidentalis.

Fig. 1. Dissection, showing slime gland, alimentary canal, and salivary gland. × 5½.
2. Dissection, female, showing reproductive organs and nephridia. × 5½.
3. Dissection, male, showing reproductive organs and crural glands. × 5½.
4. Photomicrograph. Transverse section, showing large seminal vesicle lying above alimentary canal and crural papilla retracted.
5. Longitudinal section. Salivary gland. × 400.
6. Inner face of body-wall in freshly dissected specimen, showing arrangement of main tracheæ. The piece extends across the two ventral nerve-cords, and laterally up one side and beyond the mid-dorsal line. The positions of three legs are shown (N). × 20.
7. Alimentary canal-wall under low power, showing tracheæ branching. × 96.
8. Tracheal branching. × 640.
9. Tracheal tube, showing spiral thickening. × 800.
10. Section through crural gland. × 160.
11. Nephridium in longitudinal section, showing cilia. × 240.
12. Photomicrograph of ciliated part of nephridium.
13. Opening of vas deferens into vesicula seminalis, section to show structure of wall. × 200.
14. Photomicrograph of section through vesicula seminalis, showing spermatozoa and spermatogenesis.
15. Transverse section. First part of vas deferens. × 200.
16. Median part of vas deferens, with mass of spermatozoa. × 200.
17. Terminal thick-walled part of vas deferens. × 200.
18. Longitudinal section. Ductus ejaculatorius. × 200.
19. Diagrammatic transverse section in plane of last pair of legs. × 24.
20. Diagrammatic transverse section in plane where vas deferens crosses below nerve-cords posteriorly. × 24.
21. T. S. Part of wall of anal gland of male. × 240.
22. Diagram showing connections of receptacula seminis with oviducts, and ovaries. × 200.
23. T. S. Infundibular region of oviduct. × 200.
24. L. S. Wall of ovary and oviduct. × 240.
25. T. S. Duct of receptaculum seminis. × 280.

EXPLANATION OF LETTERING.

A.	Anus.
An.Gl.	Anal gland.
Cil.R.	Ciliated portion of nephridium.
Cœ.	Cœlomic cavity.
Coll.Ves.	Collecting vesicle.
Cr.Gl.	Crural gland.
Cr.Gl.′	Crural gland of 1st leg.
Cr.Gl.″	Crural gland of last leg.
Crur.pap.	Crural papilla.
Cut.	Cuticle.
Epid.	Epidermis.
Ht.	Heart.
N.	Position of leg.
N.C.	Nerve cord.
Neph.	Nephridium.
Neph.′	Ditto of 4th and 5th legs.
Or.Pap.	Oral papilla.
Ov.	Ovary.
Ovid.	Oviduct.
Ph.	Pharynx.
Rec.Sem.	Receptaculum seminis.
Rect.	Rectum.
Sal.Gl.	Salivary gland.
Sal.G.d.	Salivary gland duct.
S.V.	Seminal vesicle.
Sli.Gl.	Slime gland.
Sp.	Spermatozoa.
Tes.	Testis.
Ut.	Uterus.
Vag.	Vagina.
Vas.def.	Vas deferens.
Vas.def.r.	Vas deferens of right side.
Vas.def.l.	Ditto of left side.

21. Notes on Marine Wood-boring Animals.—I. The Shipworms (Teredinidæ). By W. T. CALMAN, D.Sc.

(Submitted for Publication by permission of the Trustees of the British Museum.)

[Received April 27, 1920: Read June 1, 1920.]

(Text-figures 1–11.)

The specimens discussed in this paper were collected, for the most part, on behalf of a Committee appointed by the Institution of Civil Engineers to inquire into the deterioration of structures exposed to sea-action. This Committee, at my suggestion, requested its correspondents at various seaports to send in specimens of animals damaging the timber of harbour works. The result has been to get together a collection of very considerable importance, both from the point of view of the practical engineer and from that of the scientific zoologist. A set of the specimens will be placed in the Museum of the Institution of Civil Engineers, and the remainder have been presented by the Committee to the British Museum (Natural History). I desire to express my sense of obligation to the members of the Committee, more especially to the Chairman, Sir William Matthews, K.C.M.G., and the Secretary, Mr. P. M. Crosthwaite, as well as to the various harbour engineers named below, by whom the specimens were collected and preserved.

In dealing with the Teredinidæ I trespass with reluctance on the domain of the malacologists. It is only the impossibility of finding a student of Mollusca ready to undertake the description of the collection that leads me to publish these notes, to which, however, the very accurate figures drawn by Miss G. M. Woodward may give some permanent value. I am indebted to my colleagues, Mr. B. B. Woodward and Mr. G. C. Robson, for much guidance and help in exploring the literature and in examining the Museum collections of Mollusca.

Many writers have commented on the difficulties that stand in the way of a systematic study of the Teredinidæ. The lack of agreement as to the characters to be regarded as generic is strikingly shown in the recent synonymy of several species, while the inconstancy of specific characters drawn from the valves of the shell was commented on long ago by Forbes and Hanley (Hist. Brit. Mollusca, i. p. 87 (1848)). These difficulties I cannot pretend to have solved, but some general considerations suggested by study of my material may be worth recording.

The changes in form of the shell-valves during growth seem to have received little attention, although several writers mention the obvious fact that the number of the striæ on the anterior and antero-median divisions of the valves increases with age. Together with this, however, there goes on a resorption of the posterior margin, beginning on the dorsal side, just behind the hinge-knob, and extending downwards. The rapidity and extent of this erosion appears to differ in different species. Inconspicuous, as a rule, in *T. navalis* *, it becomes very marked in certain tropical species. For example, in many specimens of *Teredo mannii*, mentioned below, the auricle and nearly the whole of the postero-median area have been removed, while the antero-median (vertically striated) area occupies the greater part of the surface of the valve. It may be suggested as a possibility that the absence of extensive erosion in most specimens of *T. navalis* is due to the fact that this is a short-lived and indeed almost an annual species, the individuals rarely surviving the winter, while the much larger *T. mannii* may be longer lived, the individuals perhaps surviving for several years in the warmer waters which it inhabits. From the practical point of view it would be very important to ascertain the duration of life and the rate of growth in the different species.

Genus TEREDO Linn.

Hedley (Proc. Linn. Soc. N. S. Wales, xxiii. 1898, p. 92) regarded the presence of a "cup-shaped mantle which ...... surrounds the bases of siphons and palettes" as the chief distinctive character of a genus to which he applied at first the name *Calobates* of Gould, and later (Mem. Austral. Mus. Sydney, iii. 1899, p. 508) *Nausitoria* (i. e. *Nausitora*) of Wright. Hedley states that the type of the genus *Teredo*, "according to the figures of Forbes and Hanley and other writers," entirely lacks this structure. The accompanying figure (text-fig. 1, A) is taken from a well-preserved specimen from the estuary of the Thames, for which I am indebted to Dr. W. M. Willoughby, Medical Officer of Health for the Port of London. This specimen appears to be referable, without doubt, to the typical *T. navalis* Linn. It will be seen that the base of pallets and siphons is surrounded by a fleshy collar or fold of the mantle, entirely similar to that found in *Teredo mannii* and various other species which Hedley refers to *Nausitora* or *Calobates*.

TEREDO NAVALIS Linn. (Text-fig. 1.)

Teredo navalis Linnæus, Syst. Nat. ed. x. 1758, p. 651; Forbes and Hanley, Hist. Brit. Moll. i. 1848, p. 74, pl. i. figs. 7, 8, pl. xviii. figs. 3, 4; Gatliff and Gabriel, Proc. R. Soc. Victoria, xxviii. (n. s.) 1915, p. 117.

? *Teredo pedicellata* Quatrefages, Gwyn Jeffreys, Brit. Conch. iii. 1865, p. 174, and v. 1869, pl. liv. fig. 3.

---

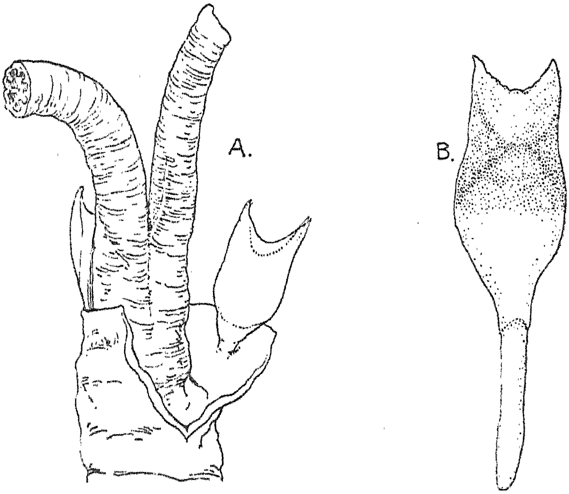
* Gwyn Jeffreys' description of the "var. *divaricata*" of *T. norvagica*, the "var. *occlusa*" of *T. navalis*, and the analogous varieties of other species, as well as the specimens named by him in the Norman collection, suggest that these varieties are based on unusually old specimens, in which the antero-median area occupies a much larger portion than usual of the surface of the valves while the auricle has been almost completely removed.

Locality.—Simon's Town, South Africa. Specimens forwarded by Lieut. L. H. A. Shadwell, R.N.V.R., Officer in charge of Works. H.M. Dockyard. From Blue Gum timber, Ordnance Jetty, E yard; from Pitch Pine, Old Ordnance Jetty, E yard; and from creosoted Danzig, A, No. 3 slip.

Remarks.—*Teredo navalis* and *T. pedicellata* have both been recorded by Gatliff and Gabriel from Victoria, but, so far as I know, neither has been recorded from South Africa.

Some of our South African specimens agree very closely, as regards the structure of the pallets, with specimens from Alderney in the Norman collection determined, apparently by Gwyn Jeffreys, as *T. pedicellata*. Jeffreys himself remarks that "this is not a satisfactory species," and the identification of his specimens with the form described by Quatrefages appears to be largely conjectural. Quatrefages's description (Ann. Sci. Nat. Zool. ser. 3, xi. 1849, p. 26) contains little to suggest it except the statement that the pallets are coloured dark brown. In the Alderney specimens and in some of those from South Africa (text-fig. 1, B), the stalk of the pallets may be as long and less than one-fourth as wide as the blade. The blade is flattened on the inner and convex on the outer surface, with the basal half calcified, white, and nearly opaque. The distal half is mostly

Text-figure 1.



Teredo navalis Linn.

A. Siphons and associated structures in a specimen from the estuary of the Thames at Gravesend. The fleshy collar at the base of the siphons has been divided and reflected, showing the insertion of the right pallet from the inner side. B. Pallet of a specimen from Simon's Town. Actual length about 5 mm.

composed of a more or less translucent horny material varying in colour from yellowish to dark brown, within which the distal end of the calcified part is seen to project as a rounded cone. On the outer surface, the central area of this horny part is occupied by a calcified plate, rectangular or irregularly rounded in outline, which reaches the distal but not the lateral margins. The distal end of the pallet is concave or notched, with a more or less deep central conical pit.

The structure described above is most easily seen in the smaller specimens from South Africa, measuring about 40 mm. in length of body and having the pallets about 5 mm. long. The Alderney specimens are a good deal smaller. In some South African specimens of about the same size, however, the distal calcified plate cannot be seen, and in some larger specimens the basal calcification, instead of penetrating into the interior of the horny part, extends up along its lateral margins. In the largest specimen of all, in which the body is a foot long, the pallets are wholly calcified, with the distal portion slightly yellowish but not horny. This large specimen does not appear to differ in any but the most trivial details from European specimens referred to *T. navalis*. The valves of the shell afford no distinctive characters.

In the absence of any more satisfactory definition of the supposed species *T. pedicellata*, all our South African specimens may be referred to *T. navalis*.

TEREDO NORVAGICA Spengler.

Teredo norvagicus Spengler, Skriv. Nat. Selsk. Kiøbenhavn, ii. H. 1, 1792, p. 102, pl. ii. figs. 4–6, B; Forbes and Hanley, Hist. Brit. Moll. i. 1848, p 66, pl. i. figs. 1–5; (*norvegica*) Calman, Marine Boring Animals, Brit. Mus. Nat. Hist. Economic Series, No. 10, 1919, p. 9, fig. 2, p. 15, fig. 5.

Teredo bruguierii Delle Chiaje, Memorie &c. iv. 1829 (1830), p. 32, pl. 54. figs. 6, 12, 13; Suter, Manual N. Z. Moll. 1913, p. 1019, pl. lv. figs. 7 *a–d*; Gatliff and Gabriel, Proc. R. Soc. Victoria, xxviii. (n. s.) 1916, p. 118, pl. xiii. figs. 9 & 12.

Remarks.—Suter recorded this species from Auckland, where, however, he considered that it was in process of being displaced by *Xylotrya saulii* (i. e. *X. australis*). It is therefore of interest to note that the latter species alone occurs in the collection which we have received from Auckland.

Suter has adopted Delle Chiaje's name for this species on the ground that Spengler's was "not binomial," and he is followed by Gatliff and Gabriel. It is true that, in the part of Spengler's memoir which deals with the genus *Teredo* (but not in that dealing with *Pholas*), the specific name is followed by a comma, not by a full stop. Those who consider this an adequate reason for displacing a name long in use and widely known will, no doubt, continue to refer to this species as *T. bruguierii*.

TEREDO MANNII Wright. (Text-figs. 2 & 3.)

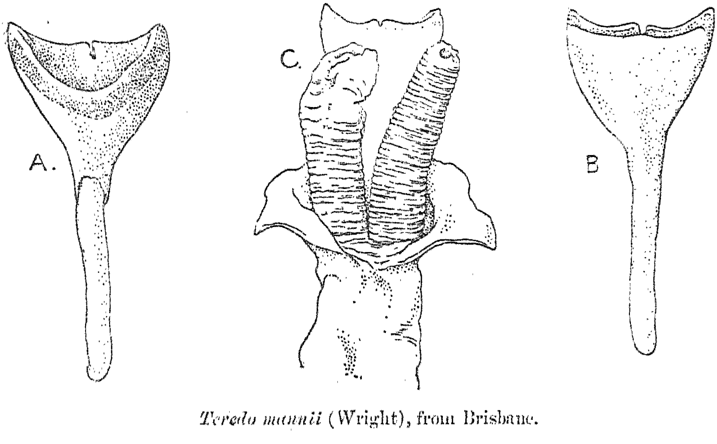
Kuphus mannii Wright, Trans. Linn. Soc. xxv. pt. 3, 1866, p. 565, pl. lxv. figs. 1–8; Hedley, Rec. Austr. Mus. iii. 1899, p. 134.

Nausitoria manni Hedley, Rep. Austr. Ass. Adv. Sci. viii. 1901, p. 248.

Locality.—Brisbane, Queensland. Specimens forwarded by Mr. E. A. Cullen, Engineer for Harbours and Rivers. From Jetties &c. in river 5 or 6 miles from Moreton Bay, in Ironbark (*Eucalyptus paniculata*) and Pine (*Araucaria cunninghamii*).

Remarks.—Of this species, already recorded by Hedley from Cooktown, in the north of Queensland, the holotype, from Singapore, is in the Museum collection. Unfortunately, it has been allowed to dry, but it has been possible, by soaking it in water, to extract the valves and pallets and to restore the siphons to something like their original form. In all the characters thus ascertained the specimens now recorded from Brisbane show a close resemblance to the holotype.

Text-figure 2.



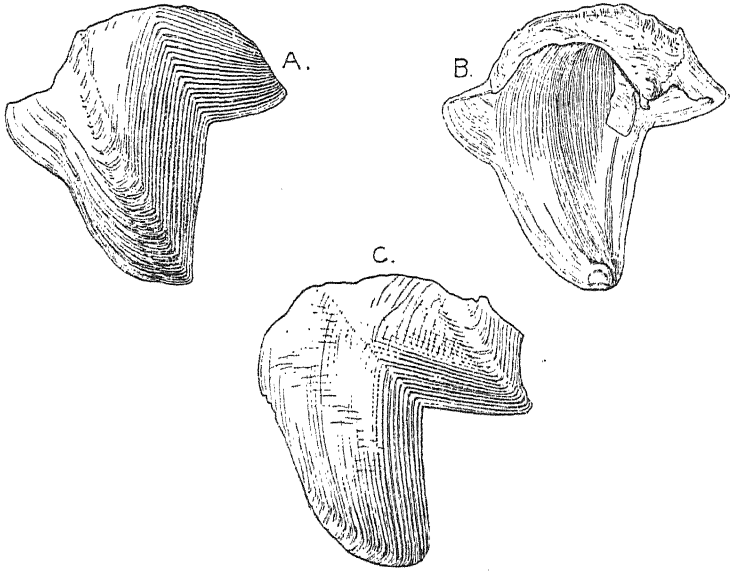
Teredo mannii (Wright), from Brisbane.

A. Outer, B. Inner surface of pallet. C. Siphons and associated structures. The fleshy collar has been divided and the right pallet removed.

The most characteristic feature of the species is the form of the pallets (text-fig. 2, A & B). The blade or expanded portion is roughly crescentic in shape. The concave distal edge has a convexity in the centre, giving it somewhat the outline of a cupid's bow, and the convexity is usually, but not always, incised by a narrow median notch. The inner surface of the blade is flat, the outer excavated distally; along the margin of the excavated area is a border of dark brown horny substance which is continued along the distal margin of the inner surface. The remainder of the surface of the blade is chalky white, and the material composing it envelops the distal end of the more translucent stalk and ends in a sharp irregular line*.

The valves of the shell in all the specimens I have examined show, to an unusual degree, the effects of secondary absorption already referred to. This is marked, not only in the dorsal region, posterior to the articular knobs, as in the valves of more normal Teredinidæ, but along the whole of the posterior margin as far as the ventral articular knob. In most specimens the whole region of the auricle has disappeared and the greater part of the postero-median region. In some specimens, as in the holotype, this latter region is represented by a narrow border along the greater part of the hind margin; in one of the specimens figured (text-fig. 3, C) it has been entirely removed

Text-figure 3.



Teredo mannii (Wright), from Brisbane.

Valves of shell. A. Right, B. Left valve of a specimen in which the eroded area (seen in B) only occupies the upper margin, while the lower part of the auricle still persists. C. Right valve of a specimen of about the same size in which the erosion extends down the posterior margin as far as the lower point of the shell and the auricle has been entirely removed.

---

* The extremely close resemblance, pointed out by Wright, between the pallets of this species and those of *Kuphus arenarius* as figured by J. E. Gray is very surprising, if the statements as to the widely different habitat of the last named species are correct.

except for a small piece near the ventral angle. In another specimen (text-fig. 3, A, B), in which the lower part of the auricle still remains, it extends only a very little below the level of the anterior division of the valve; on the inner surface it is not defined anteriorly, passing with quite unbroken surface into the postero-median division.

The siphons (text-fig. 2, C), of which the ventral, or inhalent, slightly exceeds in diameter the dorsal, or exhalent, are separate quite to the base. The fleshy collar which surrounds them is of considerable size, and, in the contracted state of the preserved specimens, conceals the siphons for about half of their length.

Genus XYLOTRYA J. E. Gray.

Xylotrya (Leach MS.) J. E. Gray, Proc. Zool. Soc. 1847, p. 188.

Whatever Leach's *Xylotrya* may have been (the reference by Menke, Syn. Méth. Moll. 2nd ed. 1830, p. 121, and the description by J. E. Gray, Syn. Brit. Mus. 44th ed. 1842, p. 76, suggest that it was the genus now known as *Xylophaga*), the name appears to have acquired validity only when Gray in 1847 referred to it the *Teredo bipalmulata* of Lamarck.

The species of the genus are for the most part sharply differentiated from those of *Teredo* by the segmented blade of the pallets. This blade is composed of a series of hollow cones successively ensheathing one another and arranged on a central axis forming a continuation of the stalk. The only approach to a transition between the two genera that I have seen is found in *Nausitora dunlopei* Wright, in which the ensheathing cones are very numerous and closely set, and appear, in the solitary type-specimen which I have examined, to be partly consolidated on the inner surface. They thus come to resemble the laminæ of which the blade is built up in some, at least, of the species of *Teredo*, differing from them, however, in their more regular arrangement *.

Many of the species referred to this genus have been only imperfectly described, and still more imperfectly figured. Possibly the two species to which new names are applied below may be identical with forms already named, but they are certainly distinct from any in the Museum collection.

XYLOTRYA AUSTRALIS, sp. n. (Text-figs. 6, 7, & 8.)

Calobates saulii Hedley, Proc. Linn. Soc. N. S. Wales, xxiii. 1898, p. 94, figs. 7–9.

Nausitoria saulii Hedley, Rep. Austr. Ass. Adv. Sci. viii. 1901, p. 248, pl. x. fig. 5.

---

* *Cf.* Fischer, Journ. Conchyl. v. 1856, p. 131.

Teredo (*Xylotrya*) *saulii* Suter, Man. N. Z. Moll. 1913, p. 1021, pl. lv. fig. 8, *a*, *b*; Gatliff and Gabriel, Proc. Roy. Soc. Victoria (n. s.) xxviii. 1916, p. 121, pl. xiii. fig. 11.

Nec *Nausitora saulii* Wright, Trans. Linn. Soc. xxv. 1866, p. 567, pl. lxv. figs. 9–15.

Localities.—Brisbane, Queensland. Specimens forwarded by Mr. E. A. Cullen, Engineer for Harbours and Rivers. From Jetties &c. in river 5 or 6 miles from Moreton Bay, in Ironbark (*Eucalyptus paniculata*) and Hardwood (*E. maculata*).

Auckland, New Zealand. Specimens forwarded by Mr. Hamer, Engineer to the Auckland Harbour Board. From Kauri and Black Butt timber.

Remarks.—Wright states that the type-specimens of his *Nausitora saulii*, which were presented to the British Museum by Miss Saul, came from Port Phillip, Australia, and it is perhaps this statement rather than any very exact correspondence with his description or figures that has led Australasian naturalists to apply the name to the species common in Australian and New Zealand waters. It appears, however, that Wright's statement was in error. The specimens in the Museum collection labelled as "Types" and presented by Miss Saul are stated, on the label and in the Register of Mollusca, to be from Callao, Peru[†]. It is true that none of the valves or pallets can be definitely recognised as the original of any one of Wright's figures, but there are two characters in which these specimens agree closely with his account; the auricle shows, on the inner surface, a series of conspicuous curved ridges indicated in Wright's pl. lxv. fig. 10, and several of the pallets have the outer surface worn away so as to expose the "central core-like body" mentioned in the description (p. 568) and shown in pl. lxv. fig. 15.

These type-specimens, however, appear to me to be specifically distinct from those I have examined from Brisbane and Auckland, which undoubtedly belong to the species called *N. saulii* by Hedley and other Australasian naturalists. The chief differences may be briefly stated as follows:—

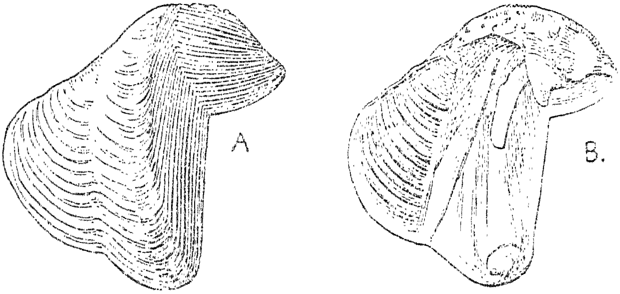
N. saulii (Wright) (text-figs. 4 & 5). Dorsal outline of valve sloping steeply without break into the upper margin of the auricle, which exceeds half the total depth of the valve and descends on the hind margin for more than half the distance from the anterior notch to the ventral edge. The auricle is marked with rather widely spaced lines of growth which, especially on the inner surface, appear as strong curved ridges. The anterior border of the auricle on the inside overlaps as a narrow band and is closely appressed to the inner surface. The pallets (text-fig. 5) have the segments strongly calcified and closely set, the average interval being estimated at not more than one-fifth

---

[*] Suter (Man. N.Z. Moll. 1913, p. 1022) mentions Callao among the localities for the species, but states that the type is from Port Phillip. I do not know the source of his information.

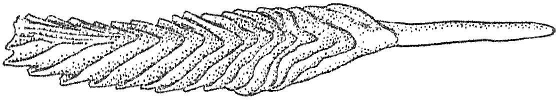
of the width. The distal edges of the segments are acutely V-shaped (this may be partly but not altogether due to their being worn away), and no trace of serration can be seen in any of the specimens. The stalk is smooth. The soft parts are unknown. The valves measure up to 7·3 mm. in length and a little less in depth.

Text-figure 4.



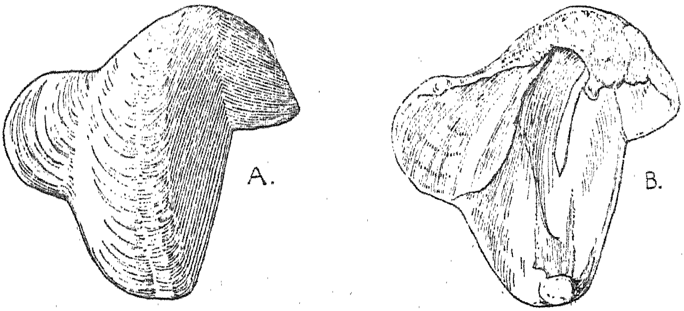
Xylotrya saulii (Wright). Syntype from Callao.
A. Right, B. Left valve of shell.

Text-figure 5.



Xylotrya saulii (Wright). Syntype from Callao. Pallet.

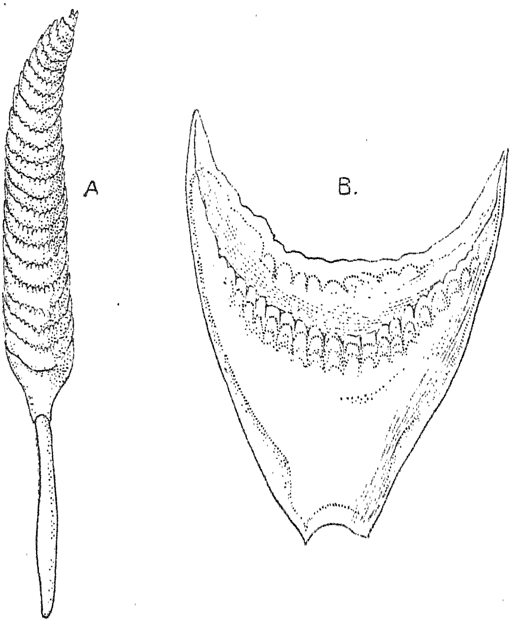
Text-figure 6.



***Xylotrya australis*, sp. n. Syntype from Auckland.**
A. Right, B. Left valve of shell.

X. australis, sp. n. (text-figs. 6, 7, & 8). Dorsal outline forming a distinct angle or concavity at the base of the auricle, which is not more than half the total depth of the valves and descends on the hind margin for not more than half the distance from the anterior notch to the ventral edge. The lines of growth on the auricle are much more closely set and less prominent, and are not at all conspicuous on the inner surface. The anterior border of the auricle on the inside overlaps as a broader band which is generally slightly raised from the inner surface. The pallets (text-fig. 7) have the segments thin and fragile and more widely spaced, the average interval being estimated at about one-third of the width. The distal margins of the segments are concave or obtusely **V**-shaped, with a delicate membranous border, at the base of which the calcified portion shows a series of coarse and somewhat irregular serrations which become very conspicuous in dried specimens. The stalk is smooth and shorter than three

Text-figure 7.

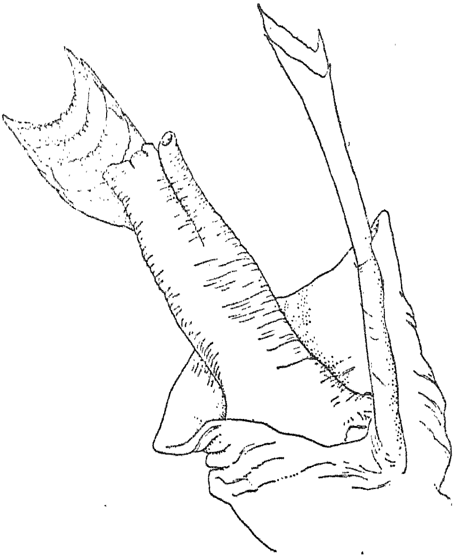


Xylotrya australis, sp. n. Syntype from Auckland.

A. External surface of pallet. B. Single segment of the pallet, further enlarged.

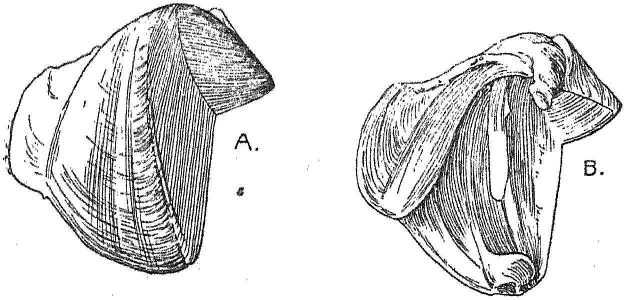
times the width of the distal part. The siphons (text-fig. 8) are adherent for two-thirds of their length in preserved specimens.

Text-figure 8.



Xylotrya australis, sp. n. Syntype from Auckland. Siphons and associated structures from the right side. The fleshy collar has been divided and reflected, the pallets remaining attached.

Text-figure 9.



Xylotrya capensis, sp. n. Syntype from Simon's Town. A. Right, B. Left valve of shell.

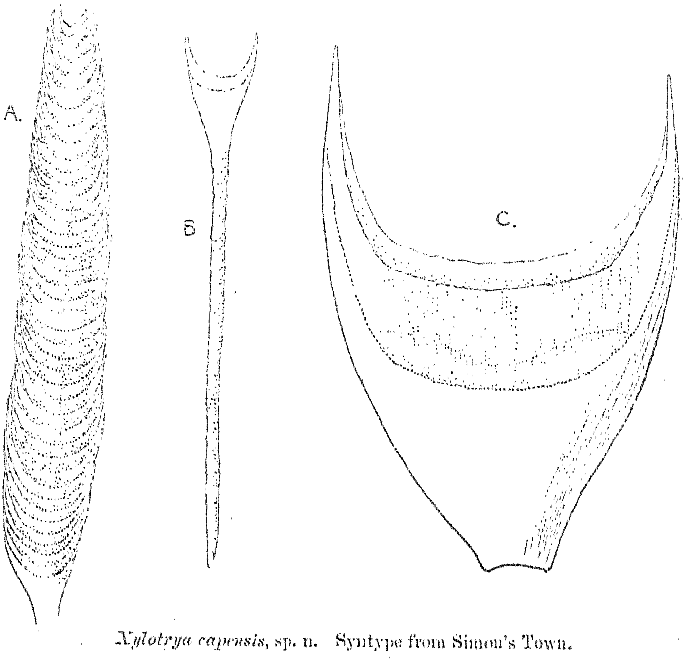
The largest complete specimen (from Auckland) is about 35 cm. long in the preserved state. The valves measure up to 13·5 mm. in length and about the same in depth.

XYLOTRYA CAPENSIS, sp. n. (Text-figs. 9, 10, & 11.)

Locality. Simon's Town, South Africa. Specimens forwarded by Lieut. L. H. A. Shadwell, R.N.V.R., Officer in charge of Works, H.M. Dockyard. From Blue Gum timber, Ordnance Jetty, E yard, and from Pitch Pine, Old Ordnance Jetty, E yard.

Description.—Valves of shell (text-fig. 9) with dorsal outline not steeply sloping posteriorly, where it is defined from the auricle by a shallow concavity. The auricle is very deep, exceeding half the total depth of the valve and extending downwards for about half the distance from the anterior notch to the ventral edge. The lines of growth on the auricle are rather closely set and not conspicuous on the inner surface. The anterior border of the auricle on the inside overlaps as a broad band, which is distinctly raised from the inner surface. The pallets (text-fig. 10) have the segments thin and fragile and closely set, the average interval being estimated at one-sixth of the width. The distal margins of the segments are regularly crescentic (on the outer surface) with a broad striated membranous border but without

Text-figure 10.



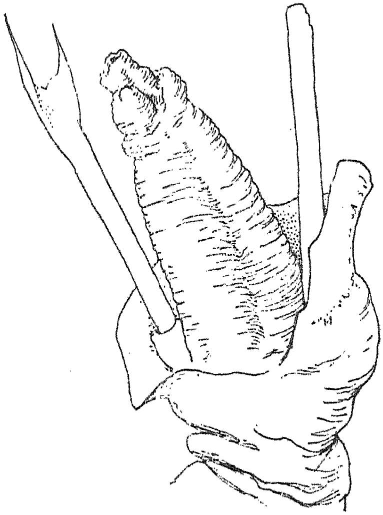
Xylotrya capensis, sp. n. Syntype from Simon's Town.

A. Distal portion of pallet. B. Stalk of pallet. C. Single segment of pallet, further enlarged.

any trace of serration. On each side the border is produced as a long filament which extends beyond three or four segments in front. The stalk is minutely roughened and, in the specimen measured, nearly five times as long as the width of the distal part. The siphons (text-fig. 11) are adherent for at least five-sixths of their length in preserved specimens.

The largest complete specimen is about 30 cm. long in the preserved state (excluding the pallets). The valves measure 12·5 mm. in length by 11·5 mm. in depth. The pallets are about 46 mm. long.

Text-figure 11.



Xylotrya capensis, sp. n. Syntype from Simon's Town.

Siphons and associated structures from left side. The fleshy collar has been divided and reflected, the pallets remaining attached.

Remarks.—In the structure of the pallets, especially in the elongated peduncle, the broad, closely-set segments, and the long lateral filaments into which they are produced, this species differs from all those of which I have seen specimens. Blainville's description of the pallets of *X. pennatifera*, with the segments "pourvues de chaque côté d'un long cil" suggests a comparison with our species. Specimens in the Museum collection referred to *X. pennatifera*, however, differ widely, having the segments but little wider than the stalk and bearing a fringe of filaments in place of the striated membranous border.

22. Report on Entozoa collected from Animals which died in the Zoological Gardens of London during Eight Months of 1919–1920. By G. M. VEVERS, M.R.C.S., L.R.C.P., F.Z.S., Beit Memorial Research Fellow, Demonstrator in Helminthology at the London School of Tropical Medicine, and Honorary Parasitologist to the Zoological Society of London.

[Received June 1, 1920: Read June 1, 1920.]

During the past eight months I have made an attempt to examine systematically for Entozoa all animals dying in the Gardens, and have attended post-mortem examinations of four hundred animals for this purpose.

Before the body was actually opened, a microscopical examination of the fæces was made, whenever practicable, for ova and embryos of Entozoa which would give some indication of the parasites harboured, and would direct attention to the particular regions for special search.

Whether this preliminary investigation gave a positive or negative result, a subsequent search of all organs was carried out.

I have also applied this method of diagnosis to living animals in the Gardens, and these examinations have in some cases given positive results. On the death of the animal the diagnosis has been confirmed by the discovery of the adult parasites; for example, the Cylichnostomes recorded from the Grevy's Zebra in the accompanying chart were detected in this manner.

Of the four hundred animals examined 76 or 19 per cent. were found to harbour parasites.

The Entozoa found fall into the following Phyla and Classes:—

		Number of Species found.	Percentage.
PLATYHELMIA.	Cestoda	15	21·40
	Trematoda	7	10·00
NEMATHELMIA.	Nematoda	45	64·40
	Acanthocephala	3	4·20
	Total	70	100·00

In all cases of Nematoda and Acanthocephala there was a preponderance of female forms. In four cases females only were found. There were 13 animals which harboured more than one species of parasite. In a Leopard Cat (*Felis bengalensis*) as many as five different species were found.

The material afforded a valuable opportunity of determining the length of life of parasites of various groups in their hosts. Very little reliable information has been gathered on this important point. The evidence given by the incidence of parasites which have intermediary hosts is, of course, more trustworthy than that of forms which have a simple life-cycle. In the latter, infection is accumulative, and may either be acquired in the paddock or be brought into the Gardens on food: thus nine examples of *Gastrodiscus aegyptiacus* were found in a Grevy's Zebra which had been in the Gardens for six years. This parasite normally occurs in Africa, and requires as an intermediary host a freshwater mollusc (*Cleopatra bulimoides*) which has not been recorded from Europe. There can be no doubt, then, that the specimens found had actually lived in the Zebra since it came from Africa, and were, therefore, over six years old.

In the same Zebra were a number of species of Bursate Nematodes, some of which have been recorded both from Africa and Europe. The life-cycle here is a simple one. That it is not possible to draw trustworthy conclusions in such a case is well illustrated by the findings in an Onager (*Equus onager*) which died quite recently. A number of the same species of parasites which occurred in the Zebra were found in this Onager, which had been born in the Gardens.

Two of the species of Cylichnostomes in the Grevy's Zebra had not been previously recorded, and it is possible that these were originally imported, but the infection may have been renewed in the paddocks. In this connection it is noteworthy that a Chapman's Zebra which died last year, after nine years in the Gardens, had only species of Bursate Nematodes which occur in European Horses.

We have, as another example of the contaminative group which might accumulate in the Gardens, an apparently unrecorded species of *Atractis* in the Elephant. Many specimens of this Nematode were found in the Indian Elephant which died in December last and which had been in the Gardens for twelve years. Recent examination of the fæces of the Elephant living in the next paddock showed that this one also is heavily infected.

The minute but fully mature females of *Atractis* are passed from time to time in the fæces, and these contain embryos so far advanced as to have the adult form. If these embryos are discharged by the mother worm in the intestine of the host, it is conceivable that they might attain sexual maturity almost immediately, and would then provide an exception to the general rule that parasitic worms do not produce a second generation of adult forms within the body of their definitive host.

The following points of especial interest were noted in individual species of Parasites:—

Two specimens of *Gnathostoma spinigerum* were obtained from the stomach of a Leopard Cat (*Felis bengalensis*). A dissection of the head-parts of a still living worm showed that the neck-glands are hollow and contractile, and contain a fluid which plays a part in altering the size of the head, thus supporting the view, as to the function of the "ballonets," recently put forward in a paper read before this Society by Baylis and Lane*.

A microscopical examination of the fæces of the same Leopard Cat showed many minute Nematode embryos. A similar examination of the stomach contents gave the same result, but no adults could be found in this or any other of the neighbouring organs. However, in the mucosa of the œsophagus and nasopharynx the same embryos were present, but here each was coiled up in an exceedingly thin membranous shell. The presence of these viviparous eggs in the nasopharynx led to the discovery of the adult worms in a most unusual position, for the frontal sinus was next explored, and here large numbers of a species of *Synthetocaulus* were found. So far as we have been able to ascertain, this species is new to science, but it is closely allied to *S. rufescens*, which occurs occasionally in the lungs and air-passages of the Sheep in Europe.

It is of interest to note that for some time before death the animal suffered from "fits" and was often seen to lose its balance and fall. These "fits," and loss of equilibrium were no doubt due to the presence of *Synthetocaulus* in the frontal sinus.

Further examination of the fæces from the same animal showed many Trematode ova, which were recognized as those of *Paragonimus westermanni*. The lungs were then searched, and four specimens of the adult fluke found. The number of eggs in the fæces was exceedingly large considering the few adults which gave rise to them.

I am indebted to Professor R. T. Leiper for his invaluable assistance and advice on a number of the more intricate points arising in the course of the above inquiry.

List of Parasites found, with their Hosts.

TREMATODA.

Genus.	*Species.*	*Host.*	*Length of time in Gardens.*
†Gastrodiscus	ægyptiacus (Cobbold, 1876). Railliet, 1898.	Grevy's Zebra. (Africa.)	6 years.
†Notocotyle	triserialis (Diesing, 1839). Diesing, 1850.	(2) Netta rufina. (India.)	1 week.
Paragonimus	westermanni (Leuckart, 1889). Stiles, 1900.	Felis bengalensis. (India.)	6 months.
Platynosoma	illiciens (Braun, 1901). Looss, 1907.	Rhamphastos erythrorhynchus. (S. America.)	3 months.

---

* P. Z. S. 1920, p. 245.

† Denotes that this Parasite has not been recorded before from this Host.

Genus.	*Species.*	*Host.*	*Length of time in Gardens.*
†Ochetosoma	formosum Nicoll, 1911.	Zamenis flagelliformis. (S. America.)	7 months.
Macrodera	naja (Rud. 1819). Looss, 1899.	Tropidonotus natrix. (Britain.)	5 months.

CESTODA.

Cyclophyllidea.

Tænia	crassicollis Rud. 1810.	Genetta genetta. (Spain.)	6 months.
Davainea	goura Fuhrmann, 1909.	Goura coronata. (New Guinea.)	1 week.
Davainea	paucitesticulata Fuhrmann, 1909.	(2) Calænas nicobarica. (Nicobar Islands.)	6 months.
Davainea	sp. inq.	Fringilla cœlebs. (Britain.)	?
Davainea	sp. inq.	Schizorhis concolor. (S. Africa.)	3 months.
Davainea	sp. inq.	Caccabis chukar. (Syria.)	10 months.
Davainea	sp. nov.	Casuarius uniappendiculatus. (New Guinea.)	6 months.
Davainea	sp. nov	Casuarius uniappendiculatus. (New Guinea.)	6 months.
Hymenolepis	villosa (Bloch, 1872). Wolffh. 1899.	Tetrax tetrax. (Britain.)	9 months.
Hymenolepis (Echinocotyle.)	sp. inq.	(4) Quelea quelea. (S. Africa.)	4 months.
Hyracotænia	procaviæ Beddard, 1912.	Procavia capensis. (S. Africa.)	3 months.
Ophiotænia	sp. inq.	Crotalus atrox. (Cent. America.)	5 months.
Tetrabothrius	cylindraceus (Rud. 1819). Diesing, 1850.	(2) Larus glaucus. (Europe.)	7 years.

Pseudophyllidea.

Dibothriocephalus sp. inq.		Conepatus proteus. (Argentine.)	2 years.

NEMATODA.

Ascaris	osculata Rud. 1819.	Otaria californiana. (North Pacific Ocean.)	6 months.
Ascaris	holoptera Rud. 1819.	(3) Testudo ibera. (S. Europe.)	1 year.
Ascaris	sp. inq.	Casarca casarca. (Europe.)	5 years.

---

† Denotes that this Parasite has not been recorded before from this Host.

Genus.	*Species.*	*Host.*	*Length of time in Gardens.*
Ascaris	sp. inq.	Spheniscus demersus. (S. Africa.)	3 weeks.
Belascaris	mystax (Zeder, 1800). Leiper, 1907.	Felis bengalensis. (India.)	6 months.
Toxascaris	sp. inq.	Vulpes lagopus. (Syria.)	2 weeks.
Porrocæcum	crassum (Deslongchamps, 1824). Raill. et Henry, 1912.	Grus communis. (Europe.)	9 years.
Contracæcum	spiculigerum (Rud. 1819). Raill. & Henry, 1912.	Phalacrocorax carbo. (Britain.)	4 months.
Oxysomatium	brevicaudatum (Zeder, 1800).	Anguis fragilis. (Britain.)	?
Heterakis	vesicularis (Dujardin, 1845).	Phasianus torquatus. (China.)	2 weeks.
Heterakis	vesicularis (Dujardin, 1845).	Ceriornis satyra. (India.)	7 years.
†Cucullanus	microcephalus (Dujardin, 1845).	Chrysema scripta rugosa. (West Indies.)	1 month.
Gnathostoma	spinigerum Owen, 1836.	Felis bengalensis. (India.)	6 months.
Ascaridia	sp. inq.	Centropus rufipennis. (India.)	10 days.
Ascaridia	lineata (Schneider, 1836).	(2) Ocyphaps lophotes. (S. Africa.)	4 years.
Physaloptera	retusa (Rud. 1819).	Tupinambis teguexin. (S. America.)	1 month.
Œsophagostomum	apiostomum Willach, 1891.	(7) Macacus rhesus. (India.)	18 months (approx.).
Ancylostomum	conepati Solanet, 1911.	Conepatus proteus. (Argentine.)	2 years.
Uncinaria	criniformis (Goeze, 1782).	Vulpes vulpes. (Britain.)	5 months.
Uncinaria	sp. inq.	Felis lynx. (Thibet.)	?
Hæmonchus	contortus (Rud. 1803).	Hippotragus equinus. (Africa.)	1 week.
Syngamus	bronchialis (Muhlig, 1884).	Casarca casarca. (Europe.)	5 years.
Cylichnostomum (Poteriostomum).	imparidentatum Quiel.	Chapman's Zebra. (Africa.)	9 years.
†Cylichnostomum	goldi Boulenger, 1916.	Chapman's Zebra. (Africa.)	"
†Œsophagodontus	robustus Giles, 1892.	Chapman's Zebra. (Africa.)	"
†Triodontophorus	intermedius Sweet, 1909.	Chapman's Zebra. (Africa.)	"

† Denotes that this Parasite has not been recorded before from this Host.

Genus.	*Species.*	*Host.*	*Length of time in Gardens.*
†Strongylus	edentatus Looss, 1901.	Chapman's Zebra. (Africa.)	9 years.
Strongylus	vulgaris Looss, 1901.	Chapman's Zebra.	"
†Probstmayria	vivipara Ransom, 1907.	Grevy's Zebra.	6 years.
†Cylichnostomum	nassatum var. parvum Yorke & Macfie, 1918.	Grevy's Zebra.	"
Strongylus	vulgaris Looss, 1901.	Grevy's Zebra.	"
Strongyloides	intestinalis Grassi, 1883.	Felis bengalensis. (India.)	6 months.
Synthetocaulus	sp. inq.	Felis bengalensis. (India.)	"
Oxyuris	equi Schrank, 1788.	Chapman's Zebra. (Africa.)	9 years.
Oxyuris	longicollis Schneider, 1866.	Testudo græca. (Europe.)	6 months.
Filaria	gracilis Dujardin, 1845.	Ateles grisescens. (S. America.)	2 months.
Setaria	sp. inq.	Hippotragus equinus. (East Africa.)	1 week.
Diplotriæna	tricuspis (Fedschenko, 1879). Raill. & Henry, 1909.	Acridotheres ginginianus. (India.)	?
Trichocephalus	affinis Rud. 1801.	Ovis vignei. (India.)	6 years.
Trichocephalus	dispar Rud. 1801.	Macacus rhesus. (India.)	18 months (approx.).
Dispharagus	squamatus (v. Linstow, 1883).	Phalacrocorax carbo. (Britain.)	4 months.
†Atractis	sp. nov.	Elephas indicus. (India.)	12 years.

ACANTHOCEPHALA.

Echinorhynchus	clavæceps.	Chrysema scripta rugosa. (America.)	1 month.
(Echinorhynchus) gen. inq.	sp. inq.	Callicebus moloch. (S. America.)	"
(Echinorhynchus) gen. inq.	sp. inq.	Leontocebus ursulus. (S. America.)	3 weeks.

† Denotes that this Parasite has not been recorded before from this Host.

23. On a Collection of Tailless Batrachians from East Africa made by Mr. A. Loveridge in the years 1914–1919.

By Miss JOAN B. PROCTER, F.Z.S.

[Received May 19, 1920: Read June 15, 1920.]

(Text-figures 1–4.)

This collection, made during the war, consists of examples of 33 species, two of which are new, representing the families Ranidæ, Engystomatidæ, and Bufonidæ*. Mr. Loveridge has presented the types of *Rappia platyrhinus* and *Megalixalus loveridgii* to the British Museum, together with specimens of the little-known species *Arthroleptis stenodactylus* Pfeff., *Rappia punticulata* Pfeff., and many others.

I am greatly indebted to Mr. Boulenger for much kind assistance in the working out of this collection.

List of Localities.

The localities fall into three divisions:—

1. BRITISH EAST AFRICA.

Nairobi.

Parklands, Nairobi.

Besil, about 50 miles south of Nairobi.

Donya Sabuk, 30 miles from Nairobi.

Thika, about 50 miles from Nairobi.

Kagiado, about 100 miles due west of Makindu, which is on the Port Florence–Mombasa Railway.

Kedong Valley, about 100 miles from Nairobi, and south of Escarpment Station on the railway.

Kenia Forest.

Tumu Tumu, on the road from Thika to Mt. Kenia.

2. EX-GERMAN EAST AFRICA (now *Tanganyika Territory*).

Gonya, about 50 miles south of Kilima-Njaro.

Longido West, about 50 miles west of Kilima-Njaro.

Amani, 40 miles from Port Zanga.

Dodoma, about 110 miles west of Morogoro, on the Dar-es-Salaam–Tanganyika Railway.

Kongwa, about 20 miles north of Mpapua.

Morogoro, about 100 miles west of Dar-es-Salaam on the railway.

Tulo, } 50 and 60 miles south of Morogoro.
Duthumi, }

---

* Pipidæ should also have been represented, but the large series of *Xenopus* collected were lost in transit.

Mhonga, about 20 miles east of Morogoro.
Dar-es-Salaam.

3. PORTUGUESE EAST AFRICA.

Lumbo.

RANIDÆ.

RANA, s. str.

1. RANA NUTTI Blgr.*

Nairobi. Morogoro. Longido West.

35 specimens. Average length of adult males 55 mm., of adult females 70 mm.; largest female 83 mm.

Snout variable both in length and in degree of acumination.

Subgenus TOMOPTERNA.

2. RANA DELALANDII Bibr.

Kagiado. Ex-G.E.A.

4 specimens. Length of adult females 41 and 45 mm.

A fine white vertebral line in one specimen; a linear vertebral groove in three specimens.

Subgenus PTYCHADENA.

3. RANA OXYRHYNCHUS Sund.

Thika. Nairobi. Morogoro. Duthumi. Gonya.

72 specimens. Average length of adult males 40 mm., of adult females 55 mm.

An extremely variable species. Snout equal to or twice as long as diameter of eye, rounded or acutely pointed, sometimes very projecting. Length of tibia $1\frac{1}{2}$ to $1\frac{2}{3}$ times in length of body, more often $1\frac{1}{2}$ times in females. Posterior corner of slit-like opening of male's vocal sac in line with lower border of arm. No light vertebral band.

4. RANA MASCARENIENSIS D. & B.

Nairobi. Gonya. Ex-G.E.A.

15 specimens. Average length of adult males 47 mm.; females half-grown.

Hind limb very variable in length, tibio-tarsal articulation reaching anywhere between eye and tip of snout; length of tibia $1\frac{2}{3}$ to $1\frac{3}{4}$ times in length from snout to vent in males, $1\frac{3}{4}$ to 2 times in females. Vocal sac of male in line with upper border of arm; 11 half-grown females have rudimentary vocal sacs. Markings very regular, the first two series of spots coinciding with the first two glandular folds, and often bisected by them; almost all specimens have a broad light vertebral band, and often a still lighter fine vertebral line in addition.

---

* "A specimen of Nutt's frog was taken at Kabete, which had retained its tail though nearly full-grown."—A. LOVERIDGE, ***Field Notes***.

Subgenus HILDEBRANDTIA.

5. RANA ORNATA Ptrs.

Ex-G.E.A.
1 specimen, ♀. Length 56 mm.
Exquisitely marked with series of dark, large, elongated spots, broad temporal bands, barred limbs; throat and breast mottled with dark brown, with the characteristic paired Y-markings.

CHIROMANTIS.

6. CHIROMANTIS XERAMPELINA Ptrs.

Ex-G.E.A.
1 specimen, probably a female. Length 66 mm.

7. CHIROMANTIS PETERSII Blgr.

Dodoma. Ex-G.E.A.
3 specimens. Length 50, 55, and 59 mm.
Inner fingers with a mere rudiment of web, outer differing from those of the type in being $\frac{1}{4}$ instead of $\frac{1}{3}$ webbed.

PHRYNOBATRACHUS.

8. PHRYNOBATRACHUS NATALENSIS Smith.

Kagiado. Nairobi. Longido West. Morogoro.
29 specimens. Average length of adults 30 mm.
An extremely variable species. Toes sometimes $\frac{2}{3}$ instead of $\frac{1}{2}$ webbed. Skin perfectly smooth or extremely warty; all male specimens from Nairobi are of the latter description, but three females from the same locality are smooth. A wide white vertebral streak in three specimens.

9. PHRYNOBATRACHUS RANOIDES Blgr.

Morogoro. Ex-G.E.A.
2 specimens. Length of larger 33 mm.

10. PHRYNOBATRACHUS BOULENGERI de Witte.

Morogoro. Duthumi. Gonya. Tulo. Ex-G.E.A.
61 specimens. Average length of adults 26 mm.
Skin perfectly smooth or warty. Markings variable, three forms with and one without vertebral bands; five specimens have a very broad vertebral band, two have a broad one, and two have a fine white vetebral line. These four forms are shown in figures of *P. natalensis* *, P. Z. S. 1907, pl. xxii.

---

* Boulenger, "Second Report on the Batrachians and Reptiles collected in South Africa by Mr. C. H. B. Grant. . . ."

11. ARTHROLEPTIS WAHLBERGII Gthr.

Morogoro. Amani.

2 specimens. Length 25 mm.

Dark without distinct markings; dermal ridge along the vertebral line. Back of one specimen covered with minute tubercles.

12. ARTHROLEPTIS WHYTII Blgr.

1 specimen. Length 35 mm.

Pale brown above, with a dark subtriangular marking between the eyes; a fine dermal ridge along the vertebral line.

13. ARTHROLEPTIS MINUTUS Blgr.

Kenia Forest. Nairobi.

33 specimens. Average length 17 mm.; large specimens 22 mm.

The majority of the specimens are dark olive, without distinct markings; four have a fine, and two a broad white vertebral line.

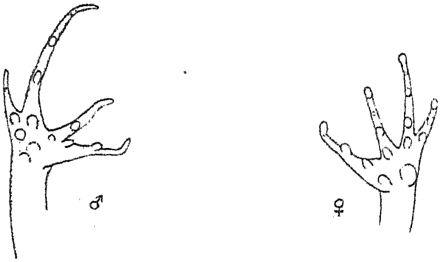
14. ARTHROLEPTIS STENODACTYLUS Pfeff.

Morogoro. Duthumi. Ex-G.E.A.

16 specimens. Average length of adults 32 mm.

This species, described by Pfeffer * from a single female from Kihengo, is new to the collection of the British Museum.

Text-figure 1.



Hand of male and female *Arthroleptis stenodactylus*. Underside, × 2.

Head broader than long; canthus rostralis obtuse; loreal region oblique, concave; interorbital width greater than that of upper eyelid; tongue with a conical papilla; tympanum distinct, usually $\frac{1}{2}$ diameter of eye. First and second fingers equal in length, third $1\frac{1}{2}$ times length of second in females, $1\frac{3}{4}$ to 2 times in males; tips of fingers and toes somewhat swollen but not dilated; toes with a rudiment of web; inner metatarsal tubercle as long as or slightly shorter than inner toe; no outer tubercle. Tibio-tarsal articulation reaches the eye or slightly beyond; length of tibia 3 times its breadth, twice in length of body. Skin smooth. Reddish brown or olive-grey above, with the dark vertebral markings characteristic of the genus; a fine white vertebral line in five, a broad one in three specimens; barred limbs; whitish beneath, sometimes with a dark throat; a few spots on lower lip. A fine linear vertebral ridge in two specimens. Males with an internal vocal sac.

---

* Jahrb. Hamb. Wiss. Anst. x. (1893) Taf. i. fig. 11.

RAPPIA *.

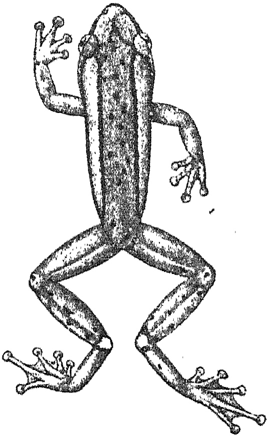
15. RAPPIA GRANULATA Blgr.

Ex-G.E.A.
6 young.

16. RAPPIA PUNCTICULATA Pfeff.

Morogoro. Ex-G.E.A.
7 specimens. Length 22 to 32 mm.

Text-figure 2.



Rappia puncticulata. Nat. size.

Interorbital space varies from $1\frac{1}{2}$ to 2 times width of upper eyelid. Fingers with a rudimentary web, toes $\frac{3}{4}$ webbed. Length of tibia $2\frac{1}{5}$ to $2\frac{1}{3}$ times its breadth, $3\frac{1}{4}$ to 4 times in length of body.

The specimen figured by Pfeffer is of a uniform colouring, with a light dark-edged lateral band passing round snout and ending on the sacral region; it has also a fine dark vertebral line. Several young in the British Museum collection have similar markings, but the seven noted above differ considerably. In these the light lateral band is heavily bordered with black, the enclosed dorsal area and upper surfaces of tibia, tarsus, and forearm irregularly spotted with black or dark grey; they have also a large white dark-edged spot on the heel. The markings of the smallest specimen are so light and indistinct that it more resembles the type specimen.

---

* "*Rappia*, sp. A Tree Frog was found impaled on the spike of an Aloe, in company with sundry grasshoppers which formed the larder of a Shrike."—A. LOVERIDGE, *Field Notes.*

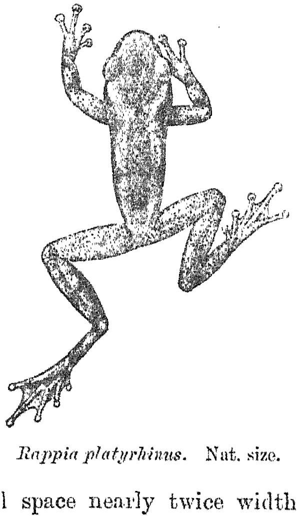
17. Rappia platyrhinus, sp. n.

Nairobi.

1 specimen, ♂.

Head small, broad as long, moderately depressed; snout flat, markedly truncate, as long as diameter of eye; canthus rostralis feebly marked; loreal region oblique, concave; nostril at end of snout; interorbital space nearly twice width of upper eyelid; tympanum hidden. Fingers long, $\frac{1}{4}$ webbed, second longer than first; toes slender, fully webbed; subarticular tubercles soft, flat, small; inner metatarsal tubercle also soft and small; no outer one. Tibio-tarsal articulation reaches middle of eye; length of tibia 5 times its breadth, $1\frac{1}{8}$ times in length from snout to vent. Skin smooth above, granular below. Uniformly brownish-grey above, finely speckled with black pigment cells which are slightly concentrated along canthus rostralis. Male with internal vocal sac and adhesive subgular disc.

Text-figure 3.



Rappia platyrhinus. Nat. size.

Measurements in millimetres.

Snout to vent	28
Head	9
Width of head	9
Snout	3
Interorbital width	3·5
1st finger	2·5
2nd ,,	3·5
3rd ,,	5
4th ,,	4
Hind limb	43
Tibia	14
Foot	19

The broad truncate snout combined with the very short web between the fingers are the distinguishing features of this species.

18. Rappia cinctiventris Cope.

Nairobi. Ex-G.E.A.

2 specimens. Length 31 and 20 mm.

Male from Nairobi greyish; female from Ex-G.E.A. pale brown, with a subtriangular dark marking; both have two paired series of small tubercles on head and shoulders. The male differs from the normal in having a subgular disc.

19. Rappia fulvovittata Cope.

Duthumi. Morogoro.

30 specimens. Average length 22 mm.

Body exceptionally elongated and depressed. Light purplish brown, with two paired dorsal streaks of a darker shade but indistinct.

20. Rappia marmorata Rapp.

Besil. Nairobi.

5 specimens. Length of largest 34 mm.

Male specimen from Nairobi is black, with three wide white dorsal bands and finely spotted sides and limbs; two females from the same locality are uniform grey, speckled with black above, salmon-pink beneath, especially hinder side of thighs; two females from Besil are uniform pale grey.

21. Rappia argus Ptrs.

Morogoro. Dar-es-Salaam.

3 specimens. Length 32 and 35 mm.

Two are light brown above; a white, black-edged band passing round snout, through eye to temple or back of head; the third has several ocellar spots on the back, but no canthal band. The absence of the characteristic spots is unusual, but there are two similar specimens in the British Museum collection. In the spotted form the canthal band is usually present and continued down the side of the body.

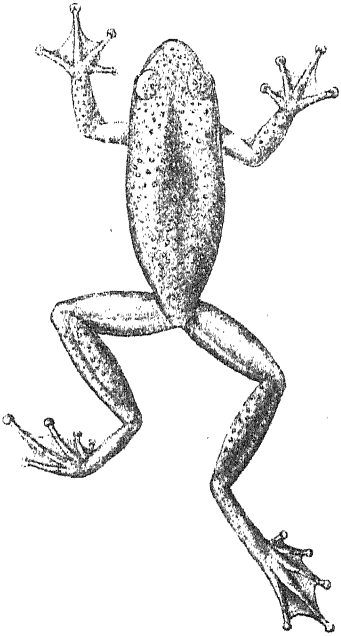
MEGALIXALUS.

22. MEGALIXALUS LOVERIDGII, sp. n.

Morogoro.

1 specimen, ♀.

Text-figure 4.



Megalixalus loveridgii. Nat. size.

Head small, depressed, broader than long; snout rather pointed, as long as diameter of eye; canthus rostralis rounded; loreal region feebly oblique; nostril near end of snout; inter-orbital width greater than that of upper eyelid; tympanum just distinguishable on right side, $\frac{1}{3}$ diameter of eye. Fingers long, $\frac{2}{3}$ webbed, the web extending as a fringe to discs of third and fourth, second longer than first, third twice length of first; toes entirely webbed; discs small and round; subarticular tubercles small, soft, feebly prominent; inner metatarsal tubercle small, soft, oval; outer one minute. Tibio-tarsal articulation reaches eye; length of tibia $4\frac{1}{2}$ times its breadth, $2\frac{1}{6}$ times in length of body. Length from snout to vent 3½ times length of head. Skin smooth, dotted with minute white tubercles each bearing a minute black spine, on upper surfaces of head, body, forearm, tibia, and hinder side of tarsus. Smooth beneath; throat granular; some small warts at corners of mouth. Pale brown above, with a faintly marked band, commencing on snout and progressively widening on the back. Uniformly speckled on upper surfaces with black pigment cells, which are slightly concentrated along the canthus rostralis; lower surfaces pale brown.

Measurements in millimetres.

Snout to vent	36
Head	11
Width of head	11·5
Snout	4·5
Interorbital width	3·5
1st finger	4
2nd ,,	5
3rd ,,	8·5
4th ,,	6
Hind limb	52
Tibia	18
Foot	23

The closest affinity of this species is *M. fornasinii* Bianconi, which it resembles in dermal characters, but which differs in having the fingers ¼ to ⅓ webbed and shorter, especially the third, which is 1½ times length of first. It is also less elongate in habit, the length from snout to vent being little over 3 times the length of the head.

CASSINA.

23. CASSINA SENEGALENSIS D. & B.

Nairobi. Ex-G.E.A.

3 specimens. Length 29, 39, and 40 mm.

Male specimens from Nairobi have a vertebral and two paired series of dark elongated spots; female from Ex-G.E.A. has five unbroken dark bands. The former have the tips of the digits much swollen, almost amounting to small discs as in *Hylambates*; specimens in the British Museum collection from the same locality show the same variation.

HYLAMBATES.

24. HYLAMBATES BOCAGII Gthr.

Nairobi.

3 specimens. Length 26, 31, and 35 mm.

Skin slightly granular above, with a linear vertebral groove. Upper parts uniform dark grey.

25. HYLAMBATES JOHNSTONI Blgr.*

Mhonga. Ex-G.E.A.
6 specimens. Length 27 to 45 mm.

ENGYSTOMATIDÆ.

PHRYNOMANTIS.

26. PHRYNOMANTIS BIFASCIATA Smith.

Ex-G.E.A. Lumbo.
3 specimens. Length 38, 40, and 48 mm.
Dark purplish brown with pink markings, agreeing with var. A of the British Museum Catalogue.

BREVICEPS.

27. BREVICEPS MOSSAMBICUS Ptrs.

Morogoro. Kongwa. Dodoma. Lumbo.
15 specimens. Length 29 to 48 mm.

HEMISUS.

28. HEMISUS MARMORATUM Ptrs.

Gonya. Morogoro.
8 specimens. Length of largest 35 mm.
Length of tibia variable, going from 2½ to 3 times in length from snout to vent. The usual occipital fold is absent in three specimens, and a linear vertebral groove is present in three specimens.

BUFONIDÆ.

BUFO.

29. BUFO REGULARIS Reuss.

Nairobi. Kedong Valley. Donya Sabuk. Tumu Tumu. Longido West. Morogoro. Duthumi. Tulo.
27 specimens. Average length of adult 80 mm.
Every specimen has either a fine light vertebral line or a sunken line in the skin; one female has its thighs marbled with red, but there are none of the beautiful red forms figured in Mr. Boulenger's Second Report on the Grant Collection †. The parotoids are very variable in length, sometimes 4 times as long as broad, and greenish in colour.

30. BUFO CARENS Smith.

Nairobi
1 specimen. Length 76 mm.

---

[*] "At Mhonga, when my boy brought me my mule which had been grazing in a patch of kaffir-corn, I was delighted to find my saddle already occupied by a large frog, whilst another was ensconced in the nose-bag."—A. LOVERIDGE, *Field Notes.*

[†] P.Z.S. 1907, pl. xxi.

24. On the Type-Specimen of *Rana holsti* Boulenger.

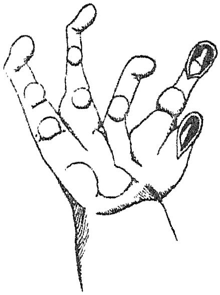
By Miss JOAN B. PROCTER, F.Z.S.

[Received June 1, 1920: Read June 15, 1920.]

(Text-figure 5.)

In "A Note on *Bambina*, the Dagger-Frog"[*], Mr. G. K. Noble states that the type-specimen of *Rana holsti* (Brit. Mus. 92.9.3.19), which is a female, has "a well-developed dagger." This is not the case. The præpollex of this specimen terminates in a knob-like tubercle not unlike the subarticular tubercles of the fingers. Even considerable pressure does not cause the protrusion of the bone within. In order to ascertain whether this female would have been able to expose a "dagger," I have dissected the præpollex of the right hand, and find that the bone, although undoubtedly very pointed, terminates over a millimetre short of the tip of the dermal tubercle; moreover, the tubercle has a thick wall, to the inner side of which the tip of the dagger is attached by soft connective tissue, forming a pad between it and the skin which shows no sign of perforation. The bone is not curved, as stated in Mr. Van Denburg's description[†].

Text-figure 5.



Right hand of *Rana holsti*. Underside, nat. size.

Dissected to show termination of bone of præpollex, and distal phalanx of first finger. (Type-specimen.)

Mr. Boulenger's description[‡]:—"A very prominent knob (rudiment of pollex) on inner side of first finger" is perfectly correct, and there was clearly no "oversight" of the dagger on his part, since such a weapon does not exist. This mistake on the part of Mr. Noble is difficult to account for, as his idea of the type-specimen was apparently derived from Dr. Stejneger *, who says: "I have had the privilege of examining the unique type-specimen, but I have nothing to add to Boulenger's original description"; a most accurate figure of the left hand is given by him.

---

[*] 'Copeia,' New York, Feb. 27, 1920, No. 79, p. 16.
[†] Proc. Cal. Ac. Sci. vol. iii. 1912, p. 197.
[‡] P. Z. S. 1913, p. 1023.

It was therefore quite a reasonable suggestion to make, even if now proved to be incorrect, that the dagger is a secondary sexual character of the male as the "aiguillons cornés et caducs qui arment le doigt interne de certains *Leptodactylus* d'Amérique et qui servent à renforcer l'amplexus pendant l'accouplement" †. In *Tympanoceros newtoni* Bocage, for another instance, the male is armed with a powerful, protruding dagger on the inner side of the first finger, whilst the female has none whatever. This point, however, is set at rest by Mr. Van Denburg, who says "the dagger is fully developed in adults of both sexes. Our collection includes females which contain eggs nearly ready for laying. These [*sic*] are armed with spurs as large and formidable as are to be found in males." This shows, therefore, that the "dagger" may, or may not, protrude externally in *R. holsti*, unless, which is unlikely, the females described by Van Denburg and Noble belong to a distinct, closely allied species.

---

* Herp. Jap., Bull. U.S. Nat. Hist. Mus. No. 58, 1907, p. 105, fig. 84.

† Boulenger, C. R. Ac. Sci. 1918, vol. clxv. pp. 987-999.

25. On the External and Cranial Characters of the European Badger (*Meles*) and of the American Badger (*Taxidea*)[*].

By R. I. Pocock, F.R.S.

[Received May 22, 1920: Read June 15, 1920.]

(Text-figures 19–25.)

CONTENTS.

	Page
Introduction	423
The Head	424
The Feet	426
The Anal and Genital Areas	428
The Skull and Teeth	432
Conclusions	434

Introduction.

Many descriptions have been published of the European and American Badgers[†], and the wide divergences between them in the structure of the skull and teeth were long ago insisted upon by Baird; but although attention has been drawn to some of the differences in external characters, it seems that dried skins have been in all cases the only material available for the purpose. So far as I am aware, no author has had the opportunity hitherto of instituting a comparison between the genera based upon fresh material; and no one appears to have questioned the right of *Taxidea* to be included in the same subfamily as *Meles*. Even Gray[‡], who split his family Melinidæ (=*Melinæ* of many recent authors) into the five tribes—Melina, Mellivorina, Mephitina, Zorillina, and Helictidina, ranged *Taxidea* alongside *Meles*, being evidently of opinion that the kinship between these two genera is closer than the kinship between *Meles* and *Arctonyx*.

As will appear in the sequel, the outcome of my comparison between the external characters—supplemented by cranial and dental characters—of the two types is to suggest that the likenesses between them are superficial, adaptive, and due to similarity of habits, and that the differences between them do not justify their relegation to the same tribe or subfamily. It will be remembered that *Mellivora* was also formerly assigned to the *Melinæ* on account of its badger-like build and feet; but the tendency of modern opinion is to regard the genus as a specialized member of the *Mustelinæ* or to place it in a subfamily apart*.

---

[*] The facts recorded in this paper are based upon specimens examined at the Society's Prosectorium.

[†] The most exhaustive and most recent description of the skull and teeth of *Meles* known to me may be found in the 'Catalogue of the Mammals of Western Europe' by Miller. The external characters, based upon an examination of dried skins, are, however, briefly dismissed. Coues gave a long and on the whole accurate description of *Taxidea* in his volume on Fur-bearing Animals, 1877.

[‡] Cat. Carnivorous etc. Mammalia, 1869, pp. 120–121. Gill (Smithsonian Misc. Coll. xi. pp. 64–66, 1872) adopted Gray's subdivisions, but converted the tribes of Melinidæ into subfamilies of the Mustelidæ. Coues followed Gill.

The Head.

The forehead is higher and rounder in *Meles* than in *Taxidea*. The *ear* of *Meles*† is moderately large with tolerably evenly rounded edge. It is simple in structure, the bursa being suppressed; the tragus is small and the antitragus scarcely developed. The supratragus (*plica principalis*) is of average size but not valvular, merely presenting a hemispherical thickening. The ear of *Taxidea* does not differ from that of *Meles* in any important particular apparently, although the lamina is less salient and its free edge is not continued inferiorly so far towards a point beneath the intertragal notch (*aditus inferior*).

The *facial vibrissæ* in *Meles* are reduced by the suppression of the interramal tuft, and the superior genal tuft is at most represented by one short bristle at least in the specimens examined. The mystacial and submental vibrissæ are moderately well developed, one of the latter on each side being exceptionally long; the inferior genal tuft is represented by one or two bristles behind the corner of the mouth and the superciliary tuft by two or more over the eye. In *Taxidea* the tufts are normal in number and situation, the genal tufts being represented by about three bristles, the upper being some distance below the level of the eye; but the interramal tuft has only about two short bristles.

The *nose* of *Meles* is produced and snout-like, and overlaps the under jaw considerably. The *rhinarium* is exceptionally large; its upper surface is naked as far back as a line behind the posterior ends of the nostrils. The anterior surface forms a wide, deep, flat disc, without trace of a median groove. The inner expanded portion of the nostril is large, the outer forms a long narrow slit extending horizontally to the lateral edge of the rhinarium. The infranarial portion is exceptionally deep and well developed both mesially and laterally; its inferior edge is convex, but varies in the degree of convexity, and is sometimes produced into a point in the middle line; but there is no philtrum and the upper lip is hairy across the middle and uncleft.

Judging from descriptions, the rhinarium of *Arctonyx*, which has been compared to that of a pig, resembles tolerably closely the rhinarium of *Meles*.

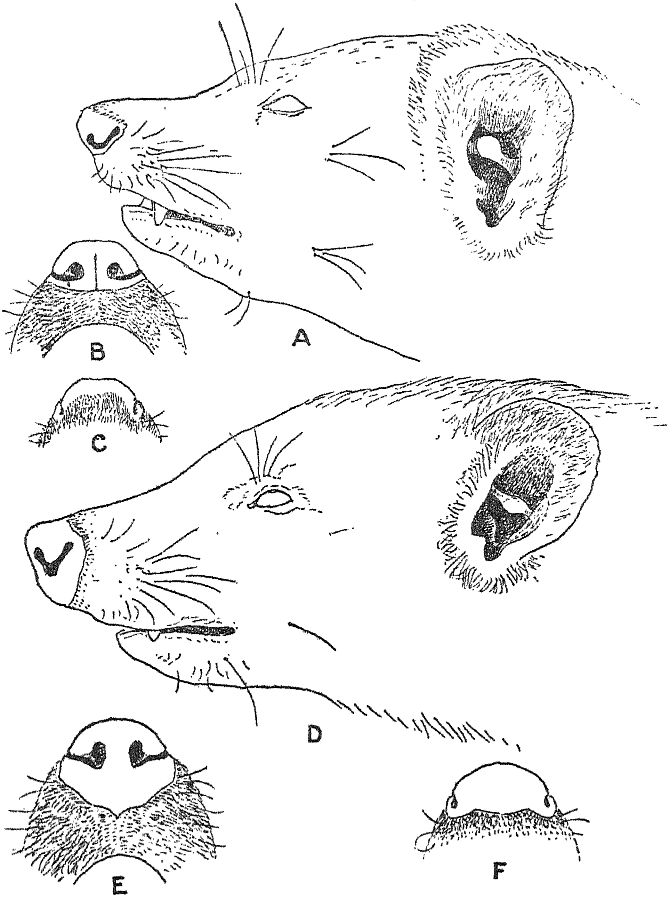
The nose of *Taxidea* is less developed and less snout-like than that of *Meles*. It does not overlap the lower jaw to the same extent, and is not so deep from the summit of the rhinarium to the edge of the upper lip. The *rhinarium* itself also differs from that of *Meles* in being covered above with hair nearly up to its anterior edge, in having an anterior median groove, and in

---

* See my paper on *Mellivora* and *Gulo* (P. Z. S. 1920, pp. 179-187).

† Figured and described by Boas, Ohrknorpel der Säug. p. 150, pl. xxi. fig. 221 (1912).

Text-figure 19.



A. Side view of head of *Taxidea americana.*
B. Rhinarium and upper lip of the same, from the front.
C. Rhinarium of the same, from above.
D. Side view of head of *Meles meles.*
E. Rhinarium and upper lip of the same, from the front.
F. Rhinarium of the same, from above.

× $\frac{1}{2}$.

(In B and E the rhinarium and upper lip are represented in the same plane, so that the lip is not foreshortened.)

having a shallow infranarial portion on each side. As in *Meles*, however, there is no philtrum, the upper lip being continuously hairy and without median groove.

The Feet.

The fore feet of *Meles*, as is well known, are essentially fossorial, the claws being of great length and far surpassing those of the hind foot. The digits are united by integument beyond the proximal end of the digital pads, and are susceptible only of slight separation. Digits 2, 3, 4, and 5 are subequally spaced, but digit 1 (pollex) is more widely separated, smaller, and set farther up the foot than digit 5. The digital pads are not well defined proximally, and the space between them and the plantar pad is quite naked. The plantar pad is wide, as wide approximately as the foot, and imperfectly four-lobed; the pollical lobe is small. Behind the plantar pad there is a large naked area, with a tuft of hair in the centre; and at the upper or proximal end of this naked area lie two carpal pads, one on each side and separated by a moderately wide space; the outer of these two pads lies near the margin of the carpus and is larger than the inner. They vary to a certain extent in size and distinctness.

The hind foot is much narrower than the fore foot and has much shorter claws. The 1st digit (hallux) is small and set higher up the foot than digit 5, which is itself a little higher than digit 2. The digits are only slightly separable, and are webbed as in the fore foot, except that digits 3 and 4 are closely united, the fusion sometimes extending to the very tip of the digital pads, although usually these pads are separated to a small extent at their distal ends. As in the fore foot, the space between the digital pads and plantar pad is quite naked, and the plantar pad is large, as wide as the foot, and indistinctly lobed. Behind it there is a large, naked, triangular area, pointed behind, which is mostly covered by the two metatarsal pads, which are sometimes separated in the middle line, sometimes fused, and are separated from the plantar pad, at least in the middle, by a narrower or broader naked area. Behind the metatarsal pads the lower surface of the foot is covered with hair.

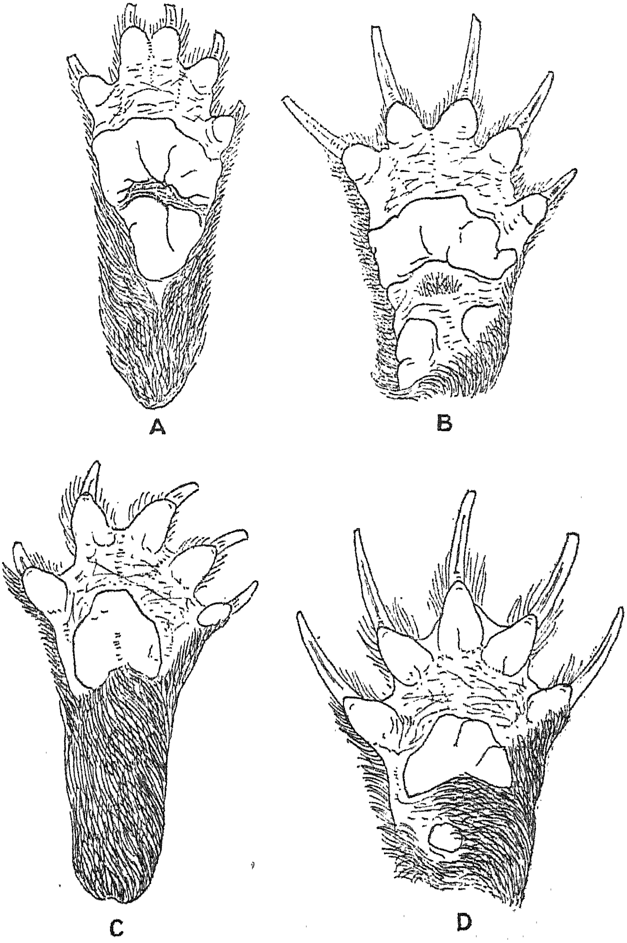
Hodgson's illustrations* of the feet of *Meles leucurus* attest their similarity to those of *Meles meles*, and unpublished sketches of the feet of *Arctonyx* by this author show that they resemble the feet of *Meles* in general features. Perhaps the plantar pads are a little narrower and more decidedly trilobate, and no mat of hair is shown on the area between the plantar and carpal pads; but two carpal pads are shown on the fore foot and two metatarsal pads in the centre of a naked area on the hind foot, but this area is larger than in *Meles* and the hairy area up to the heel is shorter.

---

* Journ. Asiatic Soc. Bengal, xvi. pl. ii. (1897). It may be noted that on this plate the sketch of the hind foot of *Helictis nipalensis* is labelled *Urva cancrivora*, and that of the latter is similarly labelled *Helictis nipalensis*.

The fore foot of *Taxidea* resembles that of *Meles* in general form, in the length and strength of the fossorial claws, and in the nakedness of the area between the digital and plantar pads;

Text-figure 20.



A. Right hind foot of *Meles meles*.
B. Right fore foot of the same.
C. Right hind foot of *Taxidea americana*.
D. Right fore foot of the same.
× ½.

but it differs in many structural details. The piriform digital pads are much larger and better defined along their proximal margin, and those of the second, third, and fourth digits are united by webbing extending past the middle of each, these three digits being closer together than the second is to the first or the fourth to the fifth, the latter being nearly at the same level as the first. Also the entire foot is wider as compared with its length, and the plantar pad is much narrower and does not occupy the whole width of the foot. It is very imperfectly divided into four lobes. The area behind it on the inner (pollical) side of the foot is partially overgrown and overlapped by hairs; on the outer side it is naked, and on the naked area a little way behind the plantar pad but towards the middle line is a single, rather small, hemispherical carpal pad, representing the inner or radial carpal pad of *Meles*. This pad is partly overlapped and, according to Coues, is sometimes overgrown by hair ('Fur-bearing Animals,' p. 266).

Similar differences, so far as the larger size of the digital pads and the greater width of the digital portion of the foot are concerned, are observable between the hind feet of the two genera; but the third and fourth digits of *Taxidea* are not so closely united, there being a definite, though narrow space between the inner proximal ends of the pads. The plantar pad is very different in *Taxidea*. It is irregularly cordate in shape and about as long as wide, and its lateral margins do not nearly extend to the edges of the feet behind the first and fifth digits. There is, moreover, no trace of metatarsal pads, the hairs of the metatarsal area reaching down to the proximal margin of the plantar pad.

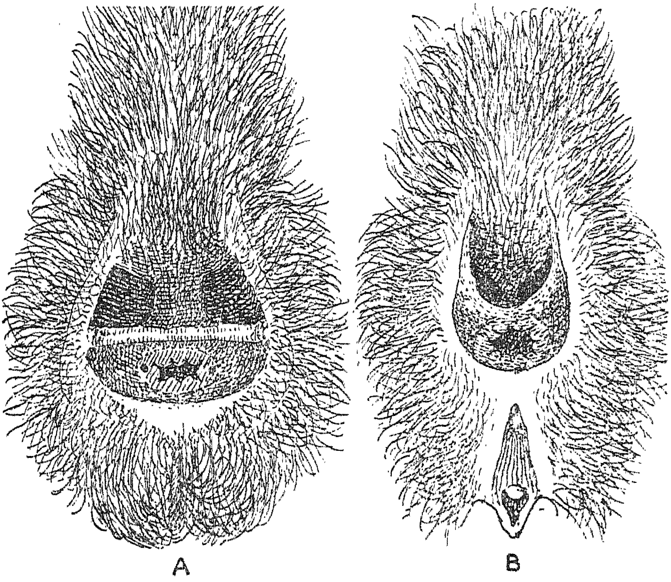
The Anal and Genital Areas.

In *Meles*, as is well known, the anus is sunk in a shallow depression, varying apparently to a certain extent in depth according to the individual. Between this and the base of the tail there is a deep subcaudal pocket, partially divided into a right and left deeper portion by a vertical partition. The inferior margin of this pouch is a transverse lamina of integument, forming the partition between it and the shallower circumanal depression. The skin of the subcaudal pouch itself is hairy and glandular *, and secretes copiously a sticky but not particularly foul-smelling fluid which stains the surrounding integument and hairs black. The true anal glands do not discharge directly into this subcaudal pouch, but just within the orifice of the anus as in all Mustelidæ. I have verified the existence of this pouch in the Japanese Badger (*M. anakuma*), and, according to M. Edwards, it is present in the Tibetan species (*M. leucurus*). It is also present in the Oriental genus *Arctonyx*, as recorded by Evans in the following passage:—"[there] is a caudal pouch directly under the origin of the tail, . . . but quite distinct from, and wholly unconnected with, the anus or genital organs. The sac is formed by duplicate folds of the common integument, having a lining of naked membrane, secreting a brown unctuous matter, not unlike cerumen, or wax of the ear"[*].

---

* As fully described by Chatin, Ann. Sci. Nat. (5) xix. pp. 106-109, pl. vii. figs. 66-67 (1874).

Text-figure 21.



A. Rear end of *Meles meles*, male, showing the subcaudal and anal pouches distended nearly to the fullest extent.

B. The same of the female, but with the pouches rather less distended transversely.

Gairdner supplements this account as follows:—"Two scent glands were found discharging into the postcaudal pocket. The secretion was brownish yellow and the hind parts were stained by the flow, and the stench so pervaded the beast that the coolies were unable to eat it"[†].

In the male of *Meles* the hairy scrotum is situated just below the rim of the circumanal sac, which, except in the middle line, is covered with short hairs. The *baculum* has been figured and described by Blumenbach* and Pohl†. It is about 4 inches long and slightly incrassate at the base, flattened and grooved beneath throughout its length and carinate above in its proximal half, then flattened and depressed, with a median dorsal groove up to the tip, which is straight or slightly upturned and expanded laterally into a roughened disc with semicircularly curved free margin. This apex is perfectly symmetrical, and an elongated slit perforating the bone behind the tip suggests that the latter results from the fusion of two short terminal processes.

---

[*] Journ. Asiatic Soc. Bengal, viii. pt. i. p. 408 (1839).

[†] Journ. Nat. Hist. Soc. Siam, i. no. 4, p. 253 (1915). From the passage quoted it appears that the secretion of the glands of *Arctonyx* is much stronger in smell than that of *Meles*. *Meles* has the habit, observable in Mongooses and Civets, with analogous glands, of rubbing the secretion on objects so that the scent is disseminated.

In the female the area around the genitalia is smooth; the genital orifice is a little below the naked rim of the circumanal sac, and opens at the summit of an inferiorly expanding groove, which ends in an angular prepuce, forming a glandular space round the small clitoris, which is strengthened with a small bone.

In *Taxidea* there is no trace either of the deep pouch immediately beneath the tail or of the shallower depression in which the anus is sunk. The anus, on the contrary, is protuberant, and in profile view stands away from the base of the tail above and from the perineal region below like a hemispherical mound‡. The anus opens just below the centre of this elevation, and the two anal glands, about the size of a hazel-nut, open within the orifice, the ducts traversing a definite papilla as in *Mephitis*. The secretion is colourless with a sweetish, not unpleasant musteline odour.

Below the anal prominence there is in the female a long naked perineal area, terminating inferiorly in a piriform prominent vulva, with the orifice above and a somewhat acuminate clitoris below. On each side of the vulva, a little below the level of the orifice, there is a glandular pocket about 6 mm. deep, from the bottom of which arise a few setæ, each planted in a shallow pit.

Thus the anal and genital areas of the female *Taxidea* differ profoundly from those of *Meles* §.

I have had no opportunity of examining a male *Taxidea*; but, according to Coues, there is a well-developed *baculum*. He describes it as "4 inches long, clubbed at one end, compressed, and with a shallow sulcus in the continuity; the other end bent

---

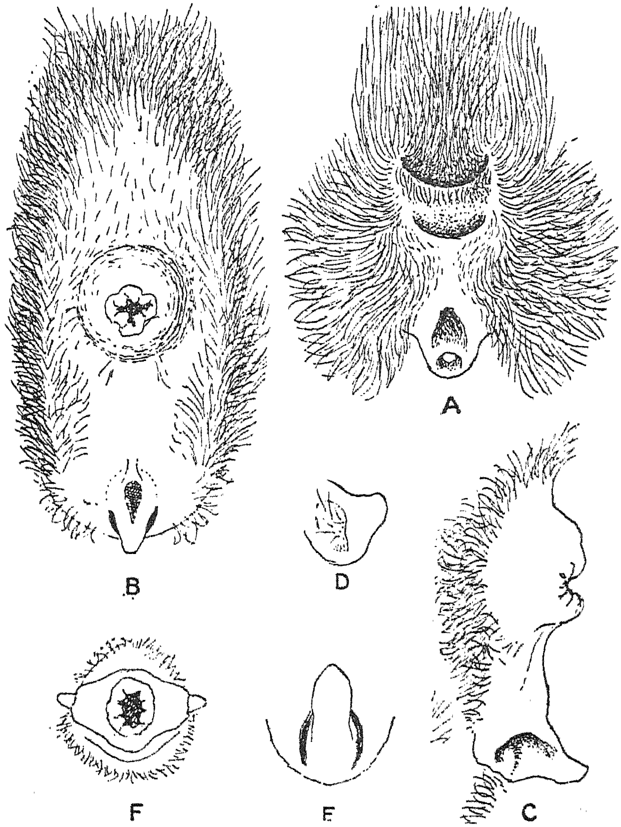
* Handbuch vergl. Anat. 1824, p. 476.

† Jena. Zeitschr. xlv. p. 385 (1909).

‡ Coues's statement (*tom. cit.* p. 267) that "the perinæal region shows, immediately beneath the root of the tail, a large transverse fissure leading into the peculiar subcaudal pouch of the *Melinæ*" is erroneous; and the error arose probably from the examination of dried skins, which were apparently all the material available for examination, judging from the bottom paragraph on p. 68 of the volume cited.

§ It is possible, however, that the difference in the size and situation of the genital orifice in the specimens examined may be more apparent than real. The examples of *Meles* were wild caught animals, one of which was known to have produced young before capture. The example of *Taxidea*, on the contrary, was received from New York as an adult specimen in 1910, and died, when an old animal, in Dec. 1918. Of her history previous to her arrival in London I know nothing, but she never bred nor was seen to pair with the male after coming to the Gardens; and it may be that the small size and low position of the genital orifice and the consequent length of the perineal area are attributable to failure of copulation and parturition.

Text-figure 22.



A. Rear end of *Meles meles*, female, with the subcaudal and anal sacs closed. × ½.
B. The same of *Taxidea americana*, female. × ½.
C. Lateral view of ano-genital area of *Taxidea*, female, showing the prominent anus and the clitoris with its lateral glandular pit partly opened. × ½.
D. The lateral gland of the clitoris of the same, opened to show the setæ at the bottom.
E. Clitoris of same, elevated to show the glandular pits closed.
F. Anus of same, spread open to show the papillæ of the anal glands.

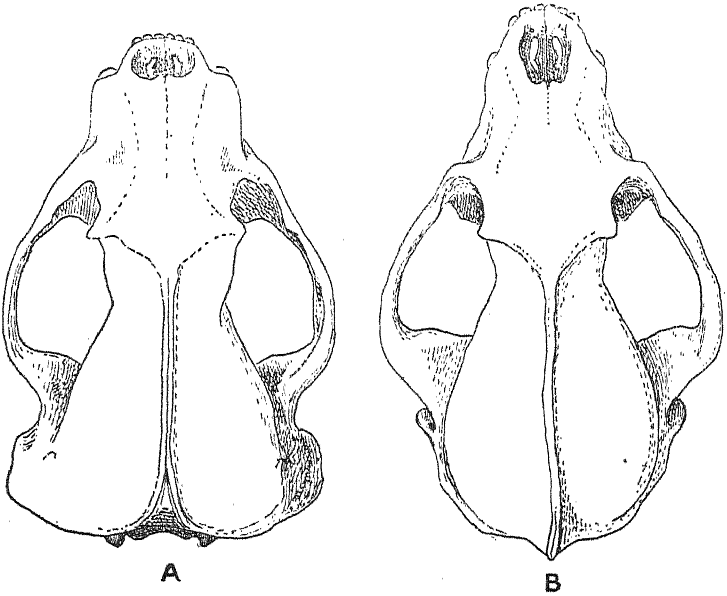
nearly at a right angle, abruptly and irregularly flattened and grooved" (*tom. cit.* p. 269).

This description is not very intelligible, and it is doubtful if the describer knew either the proximal from the distal extremity or the dorsal from the ventral surface; but I infer that the bone is compressed, grooved throughout its extent below, thickened at the base and hooked at the apex, but whether the curvature of the hook is directed upwards or downwards does not appear; and whether the apex is symmetrical or asymmetrical is also unknown.

Skull and Teeth.

The skull of *Meles meles* was fully described and illustrated by Miller; that of *Taxidea* was figured and described by Coues.

Text-figure 23.



A. Upper view of the skull of *Taxidea*. × ⅝ approx.
B. The same of *Meles*.

Elliot also reproduced photographs of it *, and Baird pointed out some of the differences between the two genera in the crania and teeth.

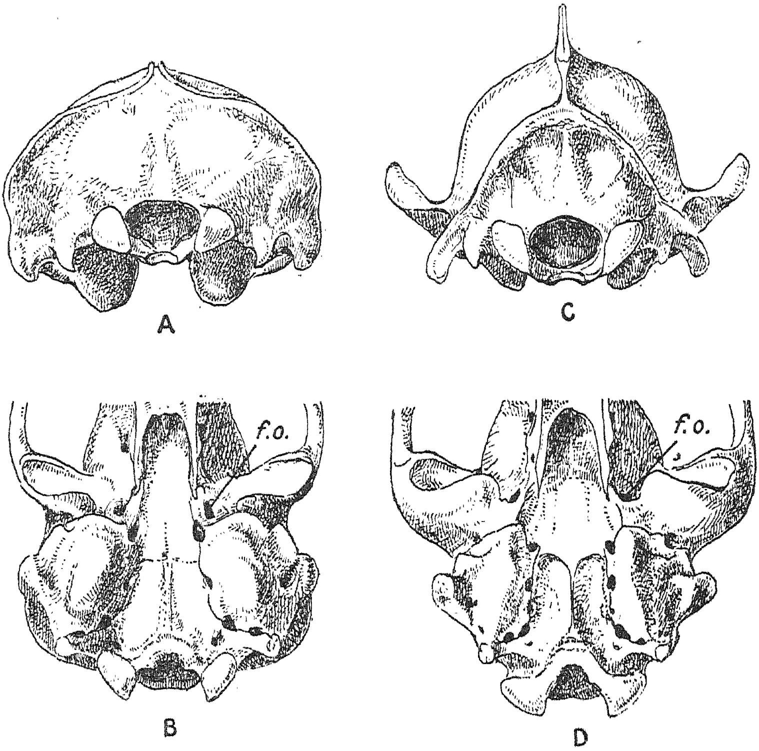
---

* Field Columb. Mus. ii. p. 320 (1901).

In the following table the principal differences are placed side by side for comparison :-

	MELES.	TAXIDEA.
Muzzle	Elongated, comparatively narrow, with prominent premaxillæ. Infraorbital foramen large, above the anterior portion of the upper molar and behind the carnassial.	Short and broad, with short premaxillæ. Infraorbital foramen small, above the anterior portion of the upper carnassial.
Zygomata	Strongly salient behind orbit; the posterior base expanded laterally and posteriorly considerably beyond glenoid.	Moderately salient behind orbit; its posterior base not expanded laterally and posteriorly beyond glenoid.
Brain-case.........	Upper surface sloping posteriorly; lateral walls rounded, converging behind zygomata. Sagittal crest high.	Upper surface hardly sloping posteriorly; lateral walls gradually divergent from orbits to occiput. Sagittal crest low or absent.
Occipital area ...	Much narrower than zygomatic width. Mastoids comparatively narrow and elongated, inclined downwards and forwards beneath the auditory meatus and lower than the glenoid. Basioccipito-sphenoidal plane inclined upwards from foramen.	Almost as wide as zygomatic width. Mastoids greatly expanded but short, not projecting below auditory meatus and about on a level with the glenoid. Basioccipito-sphenoidal plane horizontal.
Bullæ..............	Moderately inflated, scarcely below the plane of the occipital condyles and not extending forwards to the glenoid.	Much inflated, a long way below the plane of the occipital condyles and abutting against the glenoid.
Foramina	*For. rot.* concealed and opening alongside *for. lac. ant.*; *for. ov.* considerably in advance of *for. lac. med.*	*For. rot.* not concealed, opening separately from and beneath *for. lac. ant.*; *for. ov* just in front of *for lac. med.*
Teeth	*Upper carnassial* comparatively small, less than ½ area of molar. *Molar* irregularly four-sided, with two roots imbedded in cheek and two large cusps exposed in lateral view of skull; crown with one median longitudinal ridge of cusps. *Lower carnassial* with heel about as large as the anterior portion, and hollowed in the middle with two external and two internal but no median cusp; in the anterior portion of the tooth the anterior cusp is smaller than the main cusp, which is well in advance of the inner cusp.	*Upper carnassial* enormous, larger than molar. *Molar* equilaterally triangular, with one root imbedded in cheek and one cusp exposed in lateral view of the skull. Crown with two transverse rows of tubercles. *Lower carnassial* with heel about ¼ the area of the anterior portion, with one external one median, and one posterior cusp forming a transverse line; in the anterior portion of the tooth the anterior cusp is as large as the main cusp, which is in the same transverse line as the inner cusp.

Text-figure 24.



Taxidea.

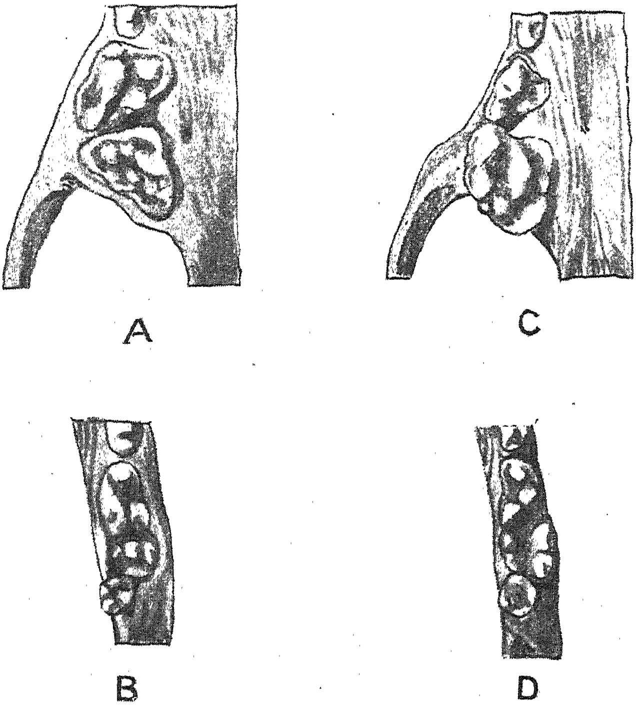
Meles.

A. Posterior view of the skull of *Taxidea*. × ⅔ approx.
C. The same of *Meles*.
B. Inferior view of posterior portion of skull of *Taxidea* (*f.o.*, *foramen ovale*).
D. The same of *Meles*.

Conclusions.

In view of the nature and number of the differences between *Meles* and *Taxidea* in skull and teeth, it seems no exaggeration to say that the resemblances between the genera in those particulars are only such as entitle them to a place in the family Mustelidæ. Unquestionably the skull of *Taxidea* presents a greater likeness to that of *Mellivora* than to the skull of *Meles*; but it is, in my opinion, by no means certain that this likeness involves close affinity, since the two genera differ considerably in the structure of the two posterior maxillary teeth and in the development of the pinna of the ear, of the pads on the feet, etc.

Text-figure 25.



A. Posterior maxillary teeth of *Taxidea*. Nat. size.
C. The same of *Meles*.
B. Posterior mandibular teeth of *Taxidea*.
D. The same of *Meles*.

Pending an examination of *Mydaus* and *Helictis**, which I have not seen, I propose to restrict the subfamily *Melinæ* to the genera *Meles* and *Arctonyx*. With these limitations the *Melinæ* may be briefly distinguished as follows from the Taxiidinæ, a new group which, for the present, contains *Taxidea* alone:—

---

* This genus, as already stated, was severed from the *Melinæ* both by Gray and Gill.

a. A well-developed subcaudal pouch; rhinarium with very deep infranarial area; plantar pads wide, carpal and metatarsal pads comparatively large, the latter on a naked area behind the plantar pad; upper carnassial much smaller than quadrilateral molar; lower carnassial with enormous heel etc.	*Melinæ.*
b. No subcaudal pouch; rhinarium with shallow infranarial area; plantar pads narrower; carpal pads much reduced, hind foot hairy down to plantar pad, metatarsal pads suppressed; upper carnassial larger than triangular molar; lower carnassial with comparatively small heel etc.	*Taxidiinæ.*

EXHIBITIONS AND NOTICES.

May 11th, 1920.

Prof. J. P. Hill, F.R.S., Vice-President, in the Chair.

The Secretary read the following Report on the Additions to the Society's Menagerie during the month of April, 1920:—

The registered additions to the Society's Menagerie during the month of April were 118 in number. Of these 39 were acquired by presentation, 15 were deposited, 28 were purchased, 32 were received in exchange, and 4 were born in the Menagerie.

The following may be specially mentioned:—

1 Chimpanzee (*Anthropopithecus troglodytes*), from West Africa, purchased on April 21st.

2 White-handed Gibbons (*Hylobates lar*), from Rangoon, received in exchange on April 15th.

2 Barbary Sheep (*Ammotragus lervia*), born in the Menagerie on April 11th.

1 Milky Eagle-Owl (*Bubo lacteus*), from Rhodesia, purchased on April 19th.

1 Banded Rail (*Hypotænidia striata*), from India, new to the Collection, purchased on April 28th.

1 Five-banded Lizard (*Mabuia quinquetæniata*), from Rhodesia, new to the Collection, deposited on April 18th.

On behalf of Messrs. E. Gerrard & Sons, Mr. R. I. Pocock, F.R.S., exhibited a mounted specimen of a pale variety of the White-bearded Gnu (*Connochætes albojubatus*), shot by Capt. Keith Caldwell, R.A., F.Z.S., in Masailand, and pointed out that apart from the general pale yellowish-brown tint, the variation affected different parts of the body in different ways, the neck-mane, the long hairs on the face, and the tail-tuft, which are normally black, being dirty white, whereas the bands on the body, making the brindled pattern, which are also normally black, were brownish red.

Miss J. B. Procter, F.Z.S., exhibited and made remarks upon a living specimen of the tailed Batrachian, *Spelerpes fuscus* Bonaparte, born on May 8th, 1920.

Prof. J. E. Duerden, F.Z.S., exhibited and made remarks upon a remarkable series of lantern-slides illustrating the sexual display and nesting-habits of the Ostrich.

June 1st, 1920.

Sir SIDNEY F. HARMER, K.B.E., F.R.S., Vice-President, in the Chair.

In the absence of Prof. R. T. LEIPER, F.Z.S., his exhibition of lantern-slides illustrating the Experimental transmission of some Helminth infections, was described by Dr. VEVERS. Specimens of *Schilbe mystus*, *Clarotes laticeps*, and *Tilapia nilotica* infected with encysted trematode larvæ, and found near Cairo, were shown. By feeding young wolves, bred in captivity, with these fishes Prof. Leiper succeeded in rearing the adult worms in enormous numbers. The cysts of *Schilbe mystus* gave rise to *Hemistoma* (*Alaria*) *alatum* of the dog, and those of *Clarotes laticeps* to *Monostoma pumilio* Looss. *M. pumilio*, which would appear to be more closely related to *Tocotrema* than to *Monostoma*, is normally a parasite of the Pelican and Kite in Egypt. That it can be reared in enormous numbers in Wolves undermines the conception of "physiological species" applied by Looss to certain trematode infections.

Dr. P. CHALMERS MITCHELL, F.R.S., gave an account, illustrated with lantern-slides, of his recent Aeroplane Trip from Cairo to Tabora, and described the character of the country passed over and the birds and mammals seen.

June 15th, 1920.

Prof. E. W. MACBRIDE, F.R.S., Vice-President, in the Chair.

The SECRETARY read the following Report on the Additions to the Society's Menagerie during the month of May, 1920:—

The registered additions to the Society's Menagerie during the month of May were 398 in number. Of these 63 were acquired by presentation, 188 were deposited, 130 were purchased, 4 were received in exchange, and 13 were born in the Menagerie.

The following may be specially mentioned:—

MAMMALIA.

1 Cheetah (*Cynælurus jubatus*), from Kilosso, Tanganyika Territory, presented by C. MacMahon, Esq., Assistant Political Officer of Kilosso, on May 1st.

2 Capybaras (*Hydrochærus hydrochærus*), bred in England, purchased on May 12th.

1 Arabian Oryx (*Oryx leucoryx*), from Central Arabia, deposited by H.M. The King on May 14th.

AVES.

2 Somali Ostriches (*Struthio molybdophanes*), purchased on May 8th.

2 White Rheas (*Rhea americana*), purchased on May 12th.

1 Kagu (*Rhinochaetus jubatus*), from New Caledonia, purchased on May 4th.

4 Long-tailed Shrikes (*Urolestes melanoleucus*) and 1 Black-collared Barbet (*Lybius torquatus*), from South Africa, deposited on May 22nd. New to the Collection.

4 Isabelline Turtle-Doves (*Turtur isabellinus*), 2 Rosy-grey Turtle-Doves (*Turtur roseigriseus*), 6 Dongola Turtle-Doves (*Turtur decipiens*), from North-East Africa, deposited on May 1st, and 2 Spotted-bellied Francolins (*Francolinus spilogaster*), presented by Major Maurice Portal, F.Z.S., on May 1st. All new to the Collection.

REPTILIA.

1 Siamese Crocodile (*Crocodilus siamensis*) and 2 Tentacled Snakes (*Herpeton tentaculatum*) from Siam, the latter new to the Collection, presented by Dr. Malcolm Smith, F.Z.S.

Prof. J. E. DUERDEN, F.Z.S., exhibited and made remarks upon a series of Ostrich eggs.

Dr. R. J. TILLYARD, M.A., D.Sc., F.L.S., F.E.S., gave an account, illustrated by lantern-slides, of The Life-history of the Dragonfly, with special reference to Australian forms Dr. Tillyard dealt first with the structure of the female ovipositor, and showed the correlation between the habit of laying eggs in the tissues of plants and the elongated form of the eggs, on the one hand, and that of laying them freely in the water, the eggs in this case being of a much more rounded form. The development of the embryo and the hatching of the larva were next dealt with; the creature that hatches from the egg is not an active larva, but a sheathed pronymph, whose existence lasts but a few seconds, and from which the active young larva emerges in its turn, representing actually the second larval instar of other insects. The various types of larvæ found in the two suborders Anisoptera and Zygoptera were next shown, and a series of slides dealt with the interesting larval specialisations in the gizzard, the prehensile labial mask, and the rectal and caudal gills.

26. On some Results of Ligaturing the Anterior Abdominal Vein in the Indian Toad (*Bufo stomaticus* Lütken).

By W. N. F. Woodland, D.Sc. (London), F.Z.S., Indian Educational Service, Senior Professor of Zoology, Muir Central College, Allahabad, U.P., India.

[Received June 1, 1920: Read October 19, 1920.]

(Text-figure 1.)

Preliminary Statement.

Most of the lower Vertebrata differ from the Mammalia in that the liver has conveyed to it a quantity of venous blood which has traversed the tissues of the legs and pelvic region, in addition to the venous blood which, as in Mammals, is derived from the gut-walls and contains the digested food products. This fact that in the lower Vertebrata the liver receives a portion of ordinary non-gut venous blood has not received the attention which its possible significance deserves. So far as I know*, only one author has ever offered an explanation, and this solely appertained to the coccygeo-mesenteric vein of Birds. Owen in 1841† made the following observations: "The venous system of the kidneys is so arranged in birds that the blood can be distributed either to the portal system by the mesenteric vein [*i.e.* the blood brought to the kidneys by the femoral veins can flow *posteriorly* through the substance of the kidneys in the so-called hypogastric veins and so enter the coccygeo-mesenteric vein], or to the pulmonary system by the vena cava and right side of the heart, according to the degree of rapidity with which the pulmonary or portal systems of veins are respectively supplied, or in other words, according to the activity with which the circulation in each of these systems may be going on at two different periods .... This disposition has been erroneously supposed to indicate that the urine was secreted from the venous blood in birds, as in reptiles and fishes; but the end attained by the venous anastomoses in question bears a much closer relation to the peculiar necessities and habit of life of the bird, and, so far as I know, has not hitherto been explained. There is no class of animals in which there may be, at any two brief and consecutive periods of existence, a greater difference in the degree of energy and rapidity with which the respiratory functions are performed than in birds. When the bird of prey, for example, stimulated by a hungry and an empty stomach, soars aloft and sweeps the air in quest of food, the muscular energies are then strained to the utmost, the heart beats with the most forcible and rapid contractions to propel the current of blood along the systemic arteries, and the pulmonary vessels require the greatest possible supply of blood to serve the heart with the due quantity of arterialized fluid: the digestive system, on the other hand, is in a state of repose, and we may conceive the portal circulation to be at its lowest ebb. Suppose the Eagle to be glutted with his quarry and reduced to a state of torpor: the animal functions are now at rest, but the organic powers concerned in the assimilation of the food are in full play, and the portal or hepatic circulation is as active as was the pulmonary a short time before." And Owen further adds that "the anastomosis of the pelvic veins, in being the means of conveying common venous blood into the liver, goes to prove that the blood of the venæ portæ does not require any peculiar preparation by circulation in the spleen or other viscera to fit it for the secretion of bile." This explanation seems plausible, especially when we reflect that the common assumption made in nearly all modern text-books to the effect that the blood always flows *anteriorly* in the so-called hypogastric veins (also sometimes called the "renal portal" veins) of the bird is almost certainly wrong, it being, on the contrary, more than probable that the blood in these veins always flows *posteriorly* *, as conjectured long ago by Jacobson (1817), Jourdain †, and other authors. But this explanation evidently does not apply to animals like Amphibia and Reptilia, which are notoriously sluggish and yet pour into their livers a much greater proportion of non-gut venous blood than birds. Also in Mammals, which most resemble Birds in the alternating activity of the respiratory and portal systems, a communication between the post-renal and portal veins does not exist.

---

* The author has not had access to literature in India.

† "On the Anatomy of the Southern Apteryx," Trans. Zool. Soc. London, vol. ii. 1841.

Now a supply of ordinary non-gut venous blood to the liver may signify (1) that the venous blood is to enable the liver to obtain a greater supply of water than it would otherwise receive, or (2) that the liver is, in part, in these forms, an organ of excretion and supplementary to the kidneys. The first supposition naturally occurs to one when Amphibia are in question, since a toad or frog certainly never drinks water by mouth, but always absorbs it by the belly and thigh skin, and this water presumably is taken to the liver by the anterior abdominal vein (and to the kidneys by the renal afferent veins), and this is probably the case in all Amphibia. Though in Fishes, Reptilia, and Birds there is no certain evidence of cutaneous absorption of water, yet it is well known that Snakes and Lizards frequently evince a desire to lie in water, and Fishes, Crocodiles, and Turtles of course habitually live in it. It may also be remarked that the anterior abdominal vein, or its equivalent, usually has factors from the walls of the urinary bladder, which, after all, is a possible source of water. Finally, it is noteworthy that, for some reason or other, Reptiles and Birds (even when aquatic) conserve their water very carefully, as we may realize when we note the semi-solid character of their urine*, the absence of sweat and mammary glands and their non-fœtal rearing of offspring; whereas Mammals, on the other hand, are very prodigal with water in all these respects. Hence it is possible that, comparatively little water being taken into the gut, the liver "arranges for" an accessory supply of blood in order to satisfy its water requirements.

---

* This is a subject I hope to investigate in the near future. It is almost certain that these so-called hypogastric veins of birds are the homologues of the "pelvic" veins of Amphibia and Reptiles and not of the "renal portal" veins, and if this be so, the blood must flow *posteriorly* in them.

† M. S. Jourdain, "Recherches sur la Veine Porte Renale." Annales des Sciences Naturelles, 4 ser., Zoologie, Tome xii. 1859, p. 134.

As to the liver, regarded as an organ of excretion in lower Vertebrata, I have no evidence.

That in the Common Frog, however (and therefore in all other animals with anterior abdominal veins), the anterior abdominal vein supply to the liver is not essential to the life of the animal is proved by the abnormalities occasionally found†, in which the anterior abdominal opens into a pre-caval instead of into a hepatic-portal vein, the animal apparently being normal in all other respects.

The Ligaturing of the Anterior Abdominal Vein in the Common Indian Toad.

While in India in 1915 and 1916, I determined to ascertain the effects of ligaturing the anterior abdominal vein, though it is evident that this operation will not give results comparable with those to be found in the abnormalities just referred to, because in the latter the blood-flow in other veins is not interfered with, while in a toad with a ligatured anterior abdominal vein the blood, which would otherwise flow through this, is forced to pass along the two renal afferent veins—the result being increased blood-pressure in the renal afferent veins and interference with the renal arterial circulation‡.

In all I performed thirty-four experiments. The method I finally adopted was to anæsthetize the toad with ether, cut through the belly skin and the underlying muscular body-wall for two or three centimetres, ligature the anterior abdominal vein in two places and remove the portion of the vein in between. Both the body-wall and the skin were sewn up with sterilized silk thread and the wound cleansed with weak carbolic acid, carbolic ointment being rubbed on the surface. While the wound was healing, I covered it with a pad of cotton wool, protected with a waterproof sheet, the four corners of which were drawn out and tied anteriorly above the scapulæ and under the animal's throat, and posteriorly over its back. The animals were given an occasional bath in shallow distilled water (the skin having previously been well cleaned), but were normally kept dry, the pad protecting the wound from urine and fæcal matter in the basin.

---

* Sharpe's statement (Amer. Jour. Physiology, vol. xxxi.) that the water of the urine of birds is absorbed in the rectum, a thick paste of uric acid remaining, is in all probability incorrect—the semi-solid urine of birds and reptiles is found in this form in the ureters, and is so secreted by the kidneys. See Appendix in my paper "On the 'Renal Portal' System (Renal Venous Meshwork) and Kidney Excretion in Vertebrata," shortly to be published.

† Woodland, W. N. F., Zool. Anzeiger, Bd. xxxv. 1910, p. 626. Also O'Donoghue, C. H., *ibid.* Bd. xxxvii. 1911, p. 36.

‡ See my paper "On the 'Renal Portal' System (Renal Venous Meshwork) and Kidney Excretion in Vertebrata," Parts I. and II., shortly to be published. The results of double perfusion and other experiments prove that as the pressure in the renal afferent veins increases, the arterial flow becomes retarded, and above a certain point is stopped altogether. Ligaturing the anterior abdominal vein in the Indian toad more than doubles the amount of blood in each renal afferent vein.

Out of 11 toads operated on as above described (save that I only ligatured the anterior abdominal vein in one place) in 1915, one lived for ten days, one for fourteen days, one a day short of eight weeks, and two others were *killed* after eight weeks and eleven weeks respectively. I shall only record my examination of the three long-period survivors, all of which were operated on on October 1st, 1915, and the wounds healed by October 12th. A day or so later they were all active and feeding well.

One, as already stated, died on November 26th, one day short of eight weeks after the operation. It was very thin, and had been ill during the previous week. It weighed at death (after subtracting weight of food in gut) 21·5 gms. The heart was normal in size (heart ratio = 229·0[*]); the liver a trifle large (liver ratio = 21·5[*]). The liver was very diseased, being full of small cysts; the spleen was much enlarged and also full of cysts, and the fat-bodies very minute. Sex not recorded. The anterior abdominal vein was found to be well ligatured and was quite empty; on the other hand, the renal afferent veins and post-caval were very large, and the two kidneys (quite healthy) were gorged with venous blood and therefore rather dark in colour. It is important to note that *a new anterior abdominal vein had not been formed*. The kidneys, after as usual being slightly squeezed and all attached vessels removed, weighed together 0·230 gm., and *were therefore apparently enormously enlarged* (kidney ratio = 93·5[*], body-weight taken at death).

The toad (a male) which I killed on November 28th—eight weeks and one day after the operation—was perfectly healthy, being active and feeding well, and all the internal organs in perfect condition. In this toad I found to my surprise that *a new vein had been formed posterior to the ligature and entering the liver, also two or three small new veins coming from the muscles of the anterior ventral body-wall and opening into the principal new vein* (text-fig. 1, B)[†]. The body-weight (after weight of food in gut subtracted) was 21·9 gms. The heart ratio was 199·3[*]; the liver (weighing exactly 1·0 gm.) ratio = 23·9[*]; the kidney ratio = 164·8[*]. The kidneys, therefore, were about normal in size.

The remaining toad (a male) I killed on December 18th—eleven weeks after the operation—and this also was in perfect health inside and out. In this toad also *a new vein had been formed* to allow the ligatured anterior abdominal to become functional. The body-weight was 30·0 gms. The heart ratio = 229·0[*]; the liver ratio = 19·6[*]; the kidney ratio = 157·9[*]. The kidneys, therefore, were about normal in size.

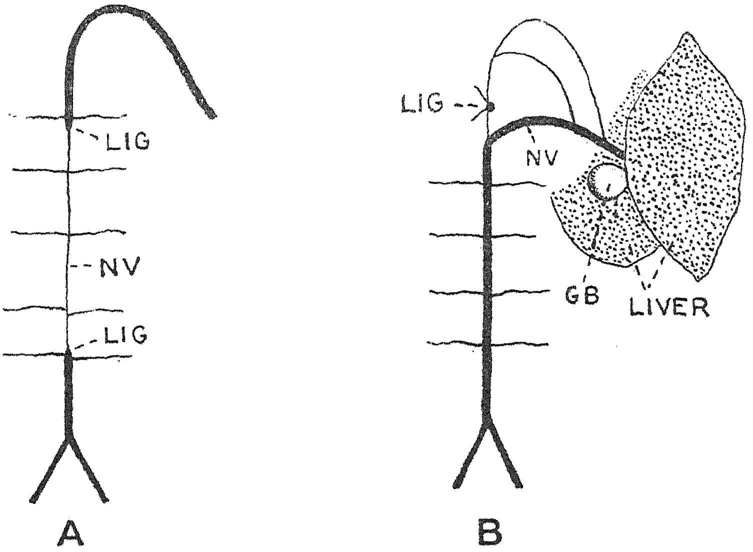
---

[*] The normal (average) ratio—$\frac{\text{Wt. of body}}{\text{Wt. of viscus}}$—for the heart (all vessels cut off and all blood washed out and dried) in these toads is 216·8 (determined in 29 toads); the normal ratio for the liver (squeezed and dried) was 28·4 (18 toads); the normal ratio for the kidneys (wt. of both kidneys, attached ureters and vessels being removed) was 237·5 (82 toads). I must add, however, that in two other lots of toads the average kidney ratios were 155·2 (10 toads) and 159·3 (6 toads). The kidney ratio (also the heart and liver ratios) shows great variations, not connected with the time of year or with sex.

[†] Compare the "rapid formation of a collateral circulation so that the blood could get round the ligature to the liver" (Starling, 'Principles of Human Physiology,' 1912, p. 858) when in a mammal the portal vein was ligatured off from the liver and made to open into the posterior vena cava. In this case, however, the liver is deprived of blood from the gut and not merely of an additional supply of ordinary venous blood, as in the toads with ligatured renal afferent veins.

In 1916 I was unfortunate in this experiment, possibly owing to my predilection for giving the animals a bath every morning, but probably also owing to the fact that in each operation I ligatured the anterior abdominal vein in two places and cut out a portion about half a centimetre in length in between. Out of 23 toads operated on only five survived for more than eleven days. That this was due largely to the mode of operation and not solely to the ligature of the anterior abdominal vein is shown by the fact that out of ten control toads in which an identical operation was performed, save that the exposed anterior abdominal vein was not ligatured, nine of them did not survive for longer than eleven days, and only one for six weeks and two days.

Text-figure 1.



A. Small regenerated anterior abdominal vein in a toad which was killed four weeks after the operation. LIG, positions of the two ligatures, the intervening portion having been cut out in the operation. NV, new vein formed.

B. Large regenerated anterior abdominal vein in a toad killed eight weeks and one day after the operation, which merely consisted of the vein being ligatured in one position. GB, gall-bladder; other-letters as in A.

I cannot guarantee the absolute fidelity of these figures, since they have been copied from rather rough sketches made when I dissected the toads.

Of the five survivors of the actual operation in 1916, one which survived eleven days had a kidney ratio (in all these ratios, unlike those of 1915, the weight of the body is that taken at date of operation) of 119·7; another which survived twelve days had a similar kidney ratio of 134·2; another survivor of two weeks and one day had a kidney ratio of 95·8. Only one toad completely survived the operation, and this was a female which I *killed* four weeks after the operation. The animal was then in perfect health inside and out, and in this case I found that *a new vein had been formed* to enable the anterior abdominal vein to continue to function (text-fig. 1, A). The animal weighed 23·4 gms. on the date of operation (July 22nd), but when killed on August 19th only weighed 14·6 gms. (after allowing for weight of food in gut). All internal organs were quite healthy, and the renal afferent veins were very large, due of course to the small size of the newly-formed portion of the anterior abdominal. The heart had apparently become much reduced in size, or was naturally small, the ratio being (weight of body at date of operation) 325·0; the liver was also extremely small (ratio=67·2); and *the kidneys were below the average size* (ratio=260·0).

Summarizing the results of these experiments, we may conclude that the ligature of the anterior abdominal vein caused either the death of the animal or the re-formation of the anterior abdominal vein: in no case did an animal survive in a healthy condition for a considerable length of time without a functional anterior abdominal vein.

Conclusions.

The fact that a new anterior abdominal vein was always formed in those toads which survived the operation described is no proof that the supply of blood to the liver by this vein is essential to the animal, because, as I have already pointed out, this feature is most certainly due to the fact that the arterial circulation in the kidneys is interfered with under the conditions of these experiments, and that is a sufficient reason for the formation of a new anterior abdominal vein.

We have also seen that frogs can live without the blood in the anterior abdominal vein being added to that in the hepatic portal vein, and this fact by itself is good evidence for the view that the non-gut blood is not essential to the animal's welfare.

Two questions remain: (1) why should an anterior abdominal vein exist? and (2) why should it normally open into the hepatic portal vein? The answer to the first question I have already indicated in a paper[*] published in 1906. In this paper I contended that in animals with "portal" kidneys the flow of blood through the primitive posterior cardinal veins is considerably hindered by the kidney tubules invading the lumina of the two veins and subdividing them up into coarse networks of sinusoids (Shore[†], Minot[‡]), and that the anterior abdominal vein is formed as an alternative route to relieve the congestion consequent on the formation of the "renal portal" system. Judging from recent measurements of the relative diameters of the renal afferent and anterior abdominal veins in *Bufo stomaticus* and *Rana temporaria* respectively, I find[§] that in the Indian toad about three-fifths of the venous blood from the legs flows to the heart via the anterior abdominal vein and about two-fifths via the two renal afferent veins, and that in the frog (*R. temporaria*) about one-half of the blood flows by each of these two routes, from which we may conclude that the resistance to flow of the blood offered by the liver capillary system is in the toad about one-third and in the frog about one-half of that offered by the renal venous meshwork ("renal portal" system) of *each* kidney. From other evidence[§]

---

[*] Woodland, W. N. F., Proc. Zool. Soc. London, 1906, p. 886.

[†] Shore, T. W., Jour. Anat. Physiology, vol. xvi. (n.s.) 1901.

[‡] Minot, C. S., Proc. Boston Soc. Nat. Hist. vol. xxviii. (10) 1898, p. 265.

[§] See Part II. of my paper "On the 'Renal Portal' System etc.," shortly to be published.

I have also concluded that the resistance offered to the blood traversing the hepatic portal system is very little more than that experienced by the blood when the anterior abdominal vein opens directly into a pre-caval vein, and this is supported by the fact that in such abnormalities (in which the anterior abdominal opens directly into a pre-caval) the renal afferent veins are of about the normal size. The renal venous meshwork in both kidneys then offering considerable resistance to the passage of blood from the hind limbs and tail, I again suggest that this blood has sought an additional path by means of which it can reach the heart without traversing the "renal portal" systems, and this suggestion is in complete agreement with the view of morphologists that the anterior abdominal vein of Amphibia and Reptilia is a "new" structure, and has nothing in common with the vein which it so often resembles--viz., the umbilical vein.

Since we have provisionally concluded that the blood in the anterior abdominal vein is of no use to the liver, and that the opening of this vein into the hepatic portal vein offers practically no more resistance to the passage of the blood than if it opened directly into a pre-caval, the answer to the second question must evidently be to the effect that the anterior abdominal vein opens into the hepatic portal vein merely because it is more convenient, the hepatic portal vein being more accessible than the pre-caval, and offering, as we have seen, but little more resistance to the flow of the blood. Occasionally, however (in "abnormal" frogs), the ancestral connection of the anterior abdominal vein with a pre-caval vein is retained. It may be added that in some animals (*e.g.*, in most Elasmobranchs) the posterior cardinal sinuses are so little broken up by the relatively small kidneys (Vialleton*) that a bypath for the blood (anterior abdominal vein) is unnecessary.

---

* Vialleton, M. L., "Caractères lymphatiques de certaines veines chez quelques Squales." C. R. Hebdom. des Séances de la Soc. Biol. Paris, Tome liv. 1902.

27. Some Observations on the Structure and Life-History of the Common Nematode of the Dogfish (*Scyllium canicula*). By J. H. LLOYD, M.Sc., F.Z.S., Assistant Lecturer and Demonstrator in Zoology at University College, Cardiff.

[Received May 15, 1920: Read November 2, 1920.]

(Text-figures 1–3.)

Introduction.

In the following pages an account is given of the parasitic Nematode, *Proleptus scillicola*, together with some observations on its life-history. The work was carried out, partly in the Zoological Department of the University of Birmingham and partly at the Marine Biological Laboratory at Plymouth, towards the end of 1914 and the beginning of 1915, but until now I have been unable to write up my results for publication, owing to my absence on military service.

I should like here to express my gratitude to Professor F. W. Gamble for his kindly criticism and advice during the course of this work. My thanks are also due to the Board of Studies in Zoology of the University of London for the use of their table at Plymouth, and to the Royal Society for providing a grant which enabled me to procure the necessary material.

A description has been thought desirable because, although the worm is exceedingly common, no complete account of its anatomy exists, and its life-history has never been worked out.

Proleptus scillicola occurs in the alimentary canal of *Scyllium canicula* from the mouth to the pyloric constriction. It has also been reported from *S. catulus* (**5**), *S. stellare* (**1**), *Raia clavata* (**1**), and *Raia circularis* (**1**). I have only had the opportunity of examining one *Scyllium catulus*, and this specimen was absolutely free from infection.

Other species of the same genus under a different generic name have been reported and briefly described as follows:—*Spiropterina inflata* (**8**) Linstow, attached to the wall of the stomach of *Scyllium immoratum*; *Spiropterina africana* (**6**) Linstow, from stomach of *Anguilla* sp. (?); *Spiropterina elegans* (**12**) Örley, from the stomach of *Hexacanthus griseus*; *Spiropterina dacnodes* (**4**) Creplin, from the œsophagus of *Raia clavata* and the stomach of *Squalus mustelus*.

The worms are white in colour, and occur either free or attached within their hosts; when attached, it is always by the tail-end.

The females are considerably larger than the males, from which they are easily distinguished by the tail, which in the male is coiled.

Historical.

Some confusion appears to exist as to the correct generic name of the Common Nematode of *Scyllium canicula*. The first generic name assigned was *Proleptus* by Dujardin (5) in 1845. He distinguished two species—*Proleptus acutus* and *Proleptus obtusus*, but as he gives neither description nor diagram of *Proleptus obtusus*, it may be considered invalid.

In 1860, Molin (**11**) described a nematode under the name of *Histiocephalus dacnodes*, which should apparently be referred to the genus *Proleptus*, as it differs considerably from the remaining species of *Histiocephalus* and appears to be wrongly placed. During the following year (1861) Van Beneden (**2**) described the worm under the generic name of *Spiropterina*.

Previous to Van Beneden placing it in a separate genus, it was provisionally assigned by Creplin (**4**) to the genus *Spiroptera*, chiefly because its head-end bore some slight resemblance to the Spiropteras of *Talpa*, *Erinaceus*, etc.

In 1870, Van Beneden (**1**) mentioned the worm under the generic name of *Coronilla*, and distinguished three new species: *Coronilla scillicola*, *Coronilla robusta*, and *Coronilla minuta*. Neither the new genus nor the new species were described, but six drawings were given, which referred indiscriminately to two of the species—viz., *Coronilla robusta* and *Coronilla scillicola*.

Spiropterina appears to be the generic name by which the worm is most commonly known, but Linstow (7) has put forward a strong argument in favour of the name *Proleptus* on the ground of priority. For this reason I shall use the generic name *Proleptus*, but as Dujardin's species *acutus* evidently refers to a distinct species which occurs in *Scyllium catulus*, and his species *obtusus* is difficult to determine, I propose to retain Van Beneden's specific name *scillicola*, and shall describe the worm under the name of *Proleptus scillicola*.

In addition to the foregoing, it has been briefly described by Linstow (**9**). My observations differ from those of Linstow in several respects, and his diagrams are inaccurate.

MORPHOLOGY.

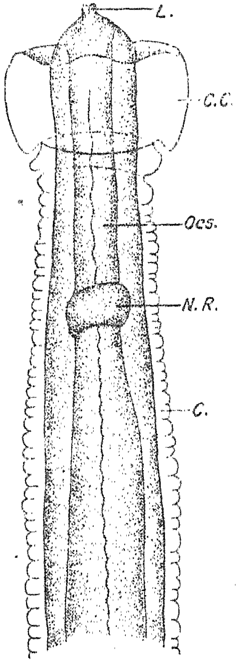
(a) *External Characters.*

The body is surrounded by a very thick, transparent cuticle, which is finely ringed transversely. *Proleptus scillicola* possesses extraordinary vitality. I have kept specimens alive in normal salt solution for over 17 weeks, whilst Linstow (**9**) records the fact that "specimens which had been in Müller's fluid for 48 hours arrived in a living condition."

The best results for whole mounts were obtained with Looss's fixative. Worms killed in this manner are straightened considerably and retain their transparency. Perenyi's fluid proved to be the best fixative for animals which were to be sectioned, whilst Para-carmine was the most effective stain.

The body is slightly attenuated towards the anterior end, and the head (text-fig. 1) is characterized by the presence of a peculiar cuticular collar. It was probably the presence of this collar which suggested to Van Beneden his generic name *Coronilla*. There are two rounded, protruding, lateral lips, each of which bears a single conical tooth. Linstow (9) mentions in addition "interiorly a small pointed cone," but I have failed to find any evidence of this either in whole mounts or sections.

Text-figure 1.



Head of *Proleptus scillicola.*

LETTERING OF FIGURES.

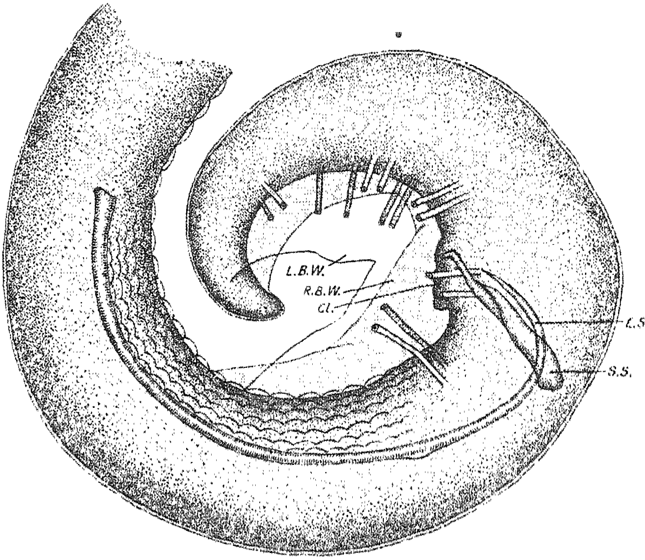
A.	Anus.	*Oes.*	Œsophagus.
Al.C.	Alimentary canal.	*Ov.D.*	Oviduct.
C.	Cuticle.	*P.*	Papillæ.
C.C.	Cuticular collar.	*R.*	Rectum.
Cl.	Cloaca.	*R.B.W.*	Right bursal wing.
C.W.	Cuticular wing.	*R.G.*	Rectal gland.
I.	Intestine.	*S.S.*	Small spicule.
L.	Lips.	*U.*	Uterus.
L.B.W.	Left bursal wing.	*Vu.*	Vulva.
L.S.	Large spicule.	*V.*	Vagina.
N.R.	Nerve-ring.		

The excretory pore is exceedingly small, and is situated in the mid-ventral line, almost as far distant posteriorly from the nerve-ring as the latter is from the anterior end.

The "tail" of the male (text-fig. 2) is coiled usually in a single ring, but occasionally into a spiral of two rings. There is an egg-shaped bursa, to right and left of which the cuticle is drawn out into wing-like expansions, supported by eight costal papillæ on each side. Van Beneden (**2**) states that there are six or seven papillæ on each side. These papillæ are pedunculate in form and are arranged symmetrically in two rows.

There is a single papilla at either end of each row; between the extreme papillæ are six others arranged in three pairs. One pair is situated in the region of the cloaca, and the two remaining pairs are posterior to it. The pre-cloacal papillæ are somewhat longer than the remainder. Linstow (**9**) has figured three papillæ on each side of the cloaca, but after careful examination of many bursæ, I have failed to discover the third papilla.

Text-figure 2.



Lateral view of tail of male *Proleptus scillicola*, showing large and small spicules and costal papillæ.

Two copulatory spicules of unequal length are present, the left being approximately five times as long as the right. The average length of the longer spicule is 2·125 mm. and of the shorter ·41 mm.

The longer spicule is curved towards the distal end, and at the beginning of the curvature there is a prominence on the convex side. Linstow (9) has stated that the larger spicule is bent into a hook at its distal end, but I have not observed this arrangement in any of the worms I have examined. It is covered with numerous transverse markings, which give it a striated appearance under a fair magnification, and attenuates to a point at its distal end. Both spicules are ensheathed in cuticle.

The "tail" of the male ends bluntly, and in the neighbourhood of the spicules the cuticle is raised into rows of rounded elevations on the ventral surface.

The tail of the female (text-fig. 3) is bent at an angle to the body and is somewhat attenuated. In the region of the vulva the cuticle increases considerably in thickness on the ventral surface and forms a pad.

Measurements in the case of *Proleptus scillicola* are almost valueless, as there are wide variations not only in the sizes of individuals, but also in the proportions of different parts. The male varies considerably less than the female.

Mature females vary in length from 32·17 mm. to 59 mm., and the tail measures from ·395 mm. to ·583 mm. The proportion of tail: total length varies from 1:75·47 to 1:146·6. Linstow has given this proportion as 1:38·7.

The distance from the vulva to the tail-end varies from ·887 mm. to 1·06 mm., and the proportion of "Vulva to tail end": total length varies from 1:39·7 to 1:53·07.

The males vary in length from 31·73 mm. to 36·2 mm. The tail measures from 1·03 mm. to 1·56 mm., and the proportion of tail: total length extends between 1:19·66 and 1:30·8. Linstow's proportion is given as 1:21·6. It would appear that Linstow has based his proportion on measurements of a single worm of each sex.

(b) *Internal Anatomy.*

The alimentary canal is normal, consisting of an œsophagus, intestine, and rectum.

The œsophagus is of unequal thickness, being approximately twice as broad behind the nerve-ring as it is in front of it. In the female it varies in length from 3·69 mm. to 5·86 mm., and the proportion of œsophagus: total length varies from 1:8·17 to 1:11·52. In the male the œsophageal length fluctuates between 3·6 mm. and 4·53 mm., and the proportion of œsophagus: total length from 1:7·32 to 1:8·81.

In transverse section the lumen of the alimentary canal is triradiate anteriorly, but towards the posterior portion of the intestine it becomes tetra-, penta-, or hexa-radiate.

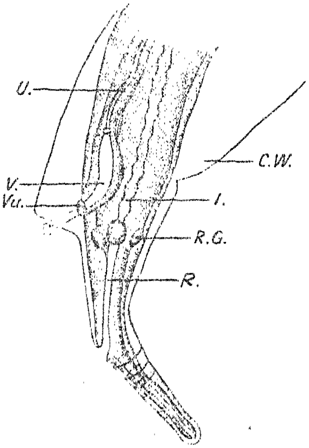
Rectal glands occur around the anterior end of the rectum in both sexes. They are four in number and are symmetrically arranged.

The female reproductive system is typical, and the vulva opens to the exterior, a short distance in front of the anus, on the ventral surface. The eggs are developed from a polynucleated mass of protoplasm, and acquire distinctness as they approach the oviduct.

The ova vary in length from 47·5 μ to 52 μ, and in breadth from 28·75 μ to 34·1 μ. The thickness of the shell varies from 6·25 μ to 6·52 μ. As a rule a coiled-up larva is formed within the shell before the "eggs" are extruded from the uterus.

It is possible to burst the "eggs" under a cover-glass and set free the contained larvæ, which average 201 μ in length. They are slightly attenuated towards the head-end, which is characterised by two protruding lips as in the adult, but there is no cuticular collar. The tail ends in a point, and is bent at an angle to the remainder of the body, but exhibits no sexual differentiation.

Text-figure 3.



Tail of mature female *Proleptus scillicola*.

The male reproductive system is of the usual type.

The excretory system consists of two canals, which pursue a sinuous course, one in each lateral line. From each canal a single branch descends to the ventral surface, where they unite just before reaching the excretory pore.

The nervous system consists of a well-defined circumœsophageal ring, which gives off numerous branches both anteriorly and posteriorly.

Life-History.

The literature dealing with the life-history of *Proleptus scillicola* is scanty. In 1865, McIntosh (**10**) described "The Trematode Larva and *Ascaris* of the *Carcinus mænas*." He discovered two specimens of his so-called *Ascaris*, one of which was lost, but his description of the other in some respects agrees with that of *Proleptus scillicola*.

In 1870, Van Beneden (**1**) stated that "Dr. McIntosh has found asexual nematodes in the 'liver' of *Carcinus mænas*, which appear to be the young of *Coronilla* (Van Beneden)."

Again, in 1875, Van Beneden (**3 a**) stated that "The ordinary crab of our coasts, *Carcinus mænas*, is the vehicle of a nematode which becomes a *Coronilla robusta* in the stomach of a ray."

Vaullegeard (**14**) in 1896 reported the larva of *Coronilla robusta* (Van Beneden) from a number of crustaceans, but stated that it was rare. In addition to *Carcinus mænas*, he discovered it in *Portunus marmoratus* Leach, *Hyas araneus* Linnæus, and *Pagurus bernhardus* Linnæus, but found only one example in each of the last three hosts. Later he found a dozen nematode larvæ in *Portunus depurator* Pennant (=*P. marmoratus* Leach).

Linstow (**9**) mentions the discoveries of McIntosh and Vaullegeard, and states that the latter distributed the preparations of the larvæ, which indubitably belong to the genus *Spiropterina* (Van Beneden).

Experimental.

Following up the suggestion of Van Beneden, I have attempted to infect the Common Shore-Crab, *Carcinus mænas*, with the larvæ of *Proleptus scillicola*.

The results so far have been disappointing, as I have succeeded in obtaining only one larva, which I may reasonably assume to have developed from eggs, taken in with mature females of *Proleptus scillicola*, on which the crabs were fed.

During the course of these experiments I have dissected 100 crabs, of which 59 were utilised in the feeding experiments and the remainder in control experiments. Of the 59 crabs used in the feeding experiments, 8 were infected with *Proleptus larvæ*, 43 larvæ being found. Two of the 41 crabs used in control experiments were infected, six larvæ being found.

Owing to the fact that all the larvæ, except one, found in the crabs used in the feeding experiments were as old or older than those found in the controls, I am bound to conclude that they occurred as the result of natural infection.

The larva which I presume to be the result of my feeding experiments measured 1·85 mm. The length of the œsophagus was ·35 mm., and the proportion œsophagus : total length was 1 : 5·28. There was no cuticular collar present, but the tail was bent at an angle to the remainder of the body.

The older larvæ examined varied in length from 10·16 mm. to 20 mm., and the length of the œsophagus from 1·79 mm. to 2·68 mm. The proportion œsophagus : total length fluctuated between 1 : 5·09 and 1 : 8·29.

In the majority of these older larvæ the head-end was surrounded by the cuticular collar which is so characteristic of the adult worm. Genital organs were absent, as was also differentiation at the tail-end.

I have dissected a number of specimens of *Pagurus bernhardus*, but have not found any larvæ of *Proleptus scillicola* in them.

Conclusions.

The above experiments show that the larvæ of *Proleptus scillicola* undoubtedly occur in *Carcinus mænas*, but my failure to produce an artificial infection seems to point to the fact that *Carcinus* is not the true intermediate host.

It is possible, however, that *Carcinus mænas* may play some part in the infection of the Dogfish. *Scyllium canicula* does not normally occur at a less depth than thirteen fathoms, whereas *Carcinus mænas* rarely occurs below a depth of three to four fathoms. During the breeding-season, however, Dogfish come close inshore, and it is probable that some of its infection takes place at this season.

Literature.

1. BENEDEN, P. J. VAN.—"Les Poissons des Côtes de Belgique, leurs Parasites et leurs Commensaux," plate 38. Mém. Acad. Sc. Bruxelles, 1871.

2. BENEDEN, P. J. VAN.—"Mémoire sur les Vers intestinaux." Compt. Rend. Acad. Sc. Paris, Suppl. 1861, pp. 270–271.

3. BENEDEN, P. J. VAN.—Les Commensaux et leurs Parasites, 1875, p. 206.

3a. BENEDEN, P. J. VAN.—Animal Parasites and Messmates. Translation of **3.** 1st English edition. London, 1875.

4. CREPLIN.—"*Spiropterina dacnodes*." Archiv für Naturgesch. 1851, p. 308.

5. DUJARDIN.—Histoire des Helminthes, 1845, p. 105.

6. LINSTOW, Dr. O. VON.—Mitteilungen aus der Zoologischen Sammlung des Museums für Naturkunde in Berlin. 1 Band, 2 Heft.

7. LINSTOW, Dr. O. VON.—Archiv für mikr. Anat. und Entwick. Band 60, 1902.

8. LINSTOW, Dr. O. VON.—Archiv für Naturgesch. Berlin, 1890. Band 1, Heft 3, pp. 180–181, Tab. x. figs. v.–viii.

9. LINSTOW, Dr. O. VON.—Achiv für mikr. Anat., Band 58. Bonn, 1901, pp. 191–194, Tab. ix. figs. 27–30.

10. MCINTOSH, W. C.—"The Trematode Larva and *Ascaris* of the *Carcinus mænas*." Q. J. M. S. vol. vi. (new series), 1865, pp. 201–204.

11. MOLIN, R.—Sitz. k. Akad. Wiss. 1860, pp. 512–513.

12. ÖRLEY.—"Die Entozoen der Haien und Rochen." Természetrajzi Füzetek, vol. ix., Budapesth, 1885, pp. 97–126 & pp. 216–220 (*Spirop. elegans*).

13. STOSSICH.—Note Elminth. Trieste, 1893.

14. VAULLEGEARD, A. — Bullet. Soc. Linnéenne de Normandie, 4 sér. t. x., 1896, pp. 50–53.

28. On the Sexual Phase in certain Indian Naididæ (Oligochæta). By Haru Ram Mehra, M.Sc., Professor of Zoology, Hindu University, Benares*.

[Received June 15, 1920: Read November 2, 1920.]

(Text-figures 1–3.)

I have recently collected in the neighbourhood of Agra a large number of examples of the following species of Naididæ and Tubificidæ, many of which are fairly common there:—

Nais pectinata var. *inæqualis* Stephenson.
Nais communis Piguet, var. *punjabensis* Stephenson.
Hæmonais laurentii Stephenson.
Chætogaster orientalis Stephenson.
Chætogaster punjabensis Stephenson.
Dero limosa Leidy.
Pristina longiseta Ehrbg.
Branchiodrilus hortensis Stephenson.
Branchiura sowerbyi Beddard.

As is well known, the Naididæ usually reproduce asexually by fission, and in many species the genital organs have never yet been described. As Stephenson remarks (**3**), if such descriptions "were available throughout the group, it can hardly be doubted that we should be able to judge better of the affinities of genera and species, and consequently to improve our classification; since the diagnoses of species and genera, and the scheme of classification, depend at present to an unduly large extent on one single set of characters, the form and distribution of the setæ." I therefore give an account of the sexual organs in two of the above species, *Nais pectinata* var. *inæqualis* and *Branchiodrilus hortensis*; though the organs have been described in certain other species of *Nais*, we have as yet no account of them in any species of the genus *Branchiodrilus*.

All the species of Naididæ which have been observed by Stephenson to become sexual in Lahore, considerably further north than Agra, do so from February to May; the rains are there later and scantier than further south, and May, June, and sometimes July, before the rains appear, when the ponds are dry and the ground baked hard, represents the most unfavourable season of the year for pond-life. In Europe these worms would seem usually to enter on the sexual phase in the autumn, before the rigours of winter. In Agra I found the sexual specimens described below in the autumn—in this part of the country the rains are abundant from the latter part of June to September; the ponds begin to dry up in October, and the cold weather appears, as in Europe, to be the unfavourable season. Whether the sexual phase makes its appearance in spring or autumn, therefore, it seems to be a measure of protection against approaching adverse conditions; the ova, quiescent or developing slowly within the cocoon, are probably able to withstand such conditions better than the adult animal.

---

* Communicated by J. Stephenson, D.Sc., F.Z.S.

In the case of *Nais pectinata* var. *inæqualis*, after the attainment of the full sexual phase, the alimentary canal in several of my specimens was seen to degenerate; the same phenomenon has been noticed by Stephenson (**3**, **4**) in *Dero limosa* and *Hæmonais laurentii*.

Many specimens of *Branchiura sowerbyi*, *Dero limosa*, *Branchiodrilus hortensis*, and *Hæmonais laurentii* were found living together in the mud of a pond near Sikandra. A similar curious association of *Branchiura sowerbyi* and a species of *Branchiodrilus* has been noted by Beddard (**1**) in the Victoria regia tank in the Royal Botanic Society's Gardens in Regent's Park; and *Branchiura sowerbyi*, *Branchiodrilus hortensis*, and a species of *Dero* have been found associated by Stephenson under natural conditions at Lahore (**2**). These three are among the few genera of Oligochæta which possess gills; in *Hæmonais laurentii*, the fourth worm which I found in the association, though there are no gills, the vascular system is, for one of the Naididæ, particularly highly developed.

NAIS PECTINATA var. INÆQUALIS Stephenson.

Since Stephenson had only spirit specimens at his command, I prefix a short account of some features of the general anatomy of this worm.

My specimens were larger than Stephenson's, their usual length being 8–10 mm., but when the worms are fully extended it may reach 15–18 mm. The colour is light reddish brown. The prostomium is bluntly conical. The worms exhibit active wriggling movements. The number of segments varies considerably—from 40 to 95.

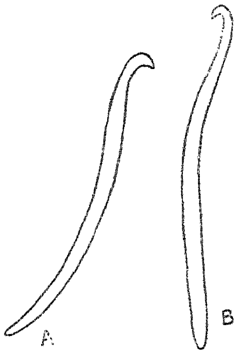
The ventral setæ are 4–6 in a bundle, usually 5; the length of those in the anterior segments (ii.–v.) is 97–105 μ, of the rest 88–93 μ. The dorsal hairs were 306–332 μ, and the dorsal needles 106–112 μ; there is a slight indication of a nodulus on the latter.

The penial setæ (text-fig. 1) are the modified ventral setæ of the sixth segment. They are 4–6 in a bundle, 98–105 μ in length, and are somewhat swollen near the tip, which is usually not forked although it is slightly hooked. Only two setæ were noted as being bifid at their free end, and in these the prongs were short, blunt, and of equal length. The whole bundle has somewhat the appearance of a fan, and arises to the inner side of the male genital aperture.

Ordinarily the dorsal setæ begin in the sixth segment, as usual in the genus. In sexually mature specimens, however, they begin in segment viii.; in one specimen there were needle setæ only in the dorsal bundles of viii., but no hairs; in a few the setæ only began in ix.; in two cases the setæ were seen to be thrown off from segment viii. when a cover-glass was gently placed over the worm,

The body-cavity contains a large number of rounded corpuscles, brownish in colour, and in addition there are a few colourless corpuscles filled with refractile granules. Cœlomic corpuscles were more numerous in specimens which had been kept in the laboratory for several days. They are few in the first six segments.

Text-figure 1.



A. Penial seta of *Nais pectinata* var. *inæqualis*. × 540.
B. Penial seta of *Branchiodrilus hortensis*. × 510.
Text-fig. 1 drawn by camera lucida.

The pharynx occupies segments iii.–v., and is diffusely covered by a small amount of chloragogen pigment, which extends right up to the prostomium. In a transverse section the cavity has the appearance of an inverted T, owing to the presence of a median dorsal diverticulum; this diverticulum and the dorsal wall of the pharynx are ciliated. On the upper and lateral surfaces of the pharynx are a number of pyriform cells, their narrow ends resting on the surface of the pharynx; these are arranged in groups of three, four, or more, and the groups are separated by strands of muscle which pass upwards from the pharynx to the body-wall. The cells are about 30 μ in length and 9 μ in thickness; they stain deeply with hæmatoxylin. The whole pharynx much resembles that of *Hæmonais laurentii* (**4**).

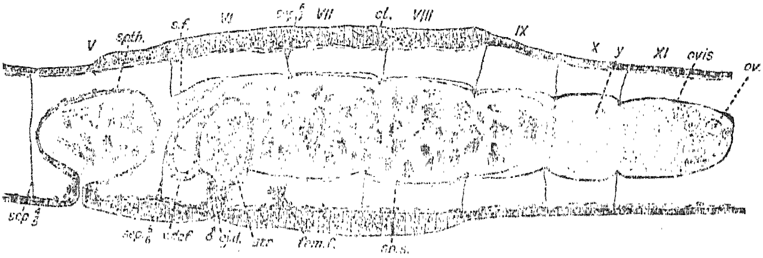
The gut is not distinctly differentiated into œsophagus, stomach, and intestine; it is somewhat larger in segments vi.–viii., then narrow as far as xiv., after which it is continued as a fairly broad tube for some distance. Its epithelium is ciliated. The anus is dorsal. Strong ciliary movements were seen in the posterior part of the gut, the direction being forwards; antiperistaltic contractions were also noticed to be taking place over some length of this part of the tube.

The blood is yellowish, and without corpuscles. The dorsal vessel lies on the left side of the alimentary canal near the ventral surface as far as septum 5/6, where it becomes dorsal, and lies over the pharynx; it is surrounded by chloragogen cells, or in the region of the pharynx by the pigment previously mentioned. It bifurcates near the anterior end of the animal, and the branches, turning ventrally, unite to form the ventral vessel at the level of the first ventral setal bundles. There are four pairs of lateral commissures in the pharyngeal region, which form a plexus; behind this, from segment vi. onwards, there is a commissure on the anterior face of each septum,—in some specimens, however, these were only seen as far back as segment xvi. The body-wall is devoid of capillaries.

The first nephridium lies in segment vii.

The cerebral ganglion is large and bilobed, deeply indented in front and behind. The ventral nerve-cord has an irregular lobulated outline, ganglia not being clearly distinguishable.

Text-figure 2.



Genital region of *Nais pectinata* var. *inæqualis*. *Atr.*, atrium; *ej.d.*, ejaculatory duct; *fem.f.*, female funnel; *ov.*, ovum; *ovis.*, ovisac; *sep.* 4/5, 5/6, and 6/7, the septa between segments iv. and v., v. and vi., and vi. and vii.; *s.f.*, seminal funnel; *sp.s.*, sperm-sac; *spth.*, spermatheca; *v.def.*, vas deferens; *y.*, yolk; ♂, male aperture. × ca. 120.

Text-figs. 2 and 3 are semidiagrammatic, and are compiled from several successive vertical sections.

Genital Organs (text-fig. 2).—As usual in the Naididæ, the gonads appear first, and disappear entirely before the rest of the genital apparatus has reached its full development.

The testes are a pair of ovoid bodies attached to the posterior face of septum 4/5. The ovaries are similar in appearance in the living specimen, but smaller; they arise from the posterior face of septum 5/6.

The seminal vesicle is formed soon after the appearance of the gonads, as a backward bulging of septum 5/6, which later on, when distended with the male products, may reach as far back as segment xii. The vas deferens, one on each side, is a short tube with only a single bend; in diameter it is 15 μ, except where it joins the atrium, where it is only 9 μ; it has a uniform lining of cubical epithelial cells. It passes vertically downwards from the funnel on the posterior face of septum 5/6, and then after a slight bend enters the atrium on its anterior aspect close to the origin of the ejaculatory duct.

The neck of the male funnel lies in the mouth of the sperm-sac (seminal vesicle). The funnels fill up the mouth of the sac, and are directed upwards and backwards just within it; they meet each other in the middle line above the gut by their inner margins, and their outer surfaces are fused with the contiguous part of the wall of the sac. They are cup-shaped, with everted lips, and are lined by columnar ciliated cells with prominent oval nuclei at the base. The greatest diameter of the funnel is about 45 μ.

The atria are ovoid chambers with their long axes vertical, lying one on each side of the seminal vesicle in segment vi. Each is 80–90 μ in height and 45–50 μ in breadth, and is lined by an epithelium of cubical cells with indistinct outlines and conspicuous nuclei; outside the epithelium is a thin coat of circular muscular fibres, outside which again the peritoneum is indicated by a few scattered nuclei. The lumen may contain spermatozoa or only a little coagulum. The ejaculatory duct is short, about 30 μ; its epithelium consists of closely packed columnar cells with large peripherally situated nuclei; it has a fairly thick investment of circular muscular fibres. The duct may be invaginated into the base of the atrial cavity; it opens to the exterior in the depth of a short tubular depression of the ventral body-wall, about 15 μ in length, which is narrower at the surface, and broader above, where it receives the duct. There are no "prostatic" cells in connection with vas deferens or atrium.

A thick band of muscle-fibres runs vertically upwards from the ventral body-wall, lying internal to the atrium and supporting the setal sac containing the penial setæ.

The ovisac, formed by the backward bulging of septum 6/7, surrounds the sperm-sac which lies within it. It may reach back to segment xvi.; it contains a large mass of yolk granules, which stain faintly with eosine; and in its hinder part a number of ova. The septa of the several segments behind the seventh retain a transverse position between the body-wall and the ovisac, fusing closely with the periphery of the latter. Large blood-vessels are seen closely applied to the sperm-sac and inner face of the ovisac.

The female funnels are attached to the anterior face of septum 6/7 near the ventral parietes; the cells lining it are small, and appear to be modified peritoneal cells containing little else than nuclei. In one specimen the funnels were seen to open on the ventral surface at about the level of septum 6/7. They are seen only in specimens which have reached full sexual maturity, and considering the large size of the ova seem to be too minute to be of any functional importance.

The spermathecæ occupy segment v., and their openings lie at the anterior edge of the clitellum immediately behind septum 4/5. The ampulla attains a maximum height of 105 μ; its posterior surface lies near the mouth of the sperm-sac, while in front it may push forwards septum 4/5 so as to encroach on segment iv. The ampullæ when distended are ovoid, and meet and press on each other in the middle line above the alimentary tube. The epithelium is low and flat, except near the duct where the cells are fairly high and cubical. There is a thin layer of circular muscular fibres, and a few peritoneal cells on the outside. The spermathecal duct arises anteriorly instead of from the middle of the base of the ampulla; it is slightly oblique in position, cylindrical, about 45 μ in length; its lining consists of closely packed columnar cells with nuclei peripheral, and a fairly thick coat of circular muscular fibres surrounds this epithelium.

The clitellum covers more than half of segment v., and all vi., vii., and viii.; to the naked eye it is opaque white. The cells are four times as high as the ordinary surface epithelium, are vacuolated, and when fully developed lose their distinctness of outline. The clitellum is absent from the regions of the body-wall between the spermathecal pores and the male apertures.

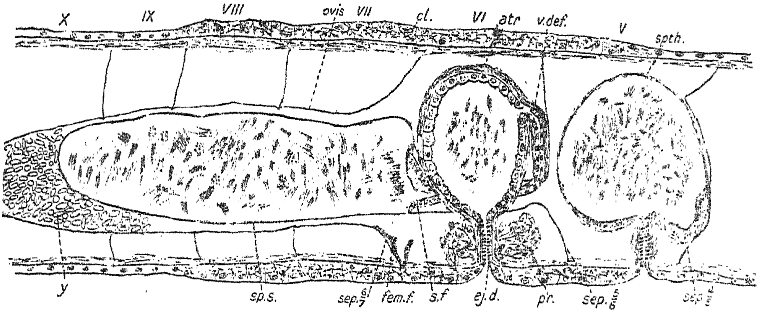
The alimentary canal undergoes great degeneration in the sexually mature worm. Though known in *Dero limosa* and *Hæmonais laurentii*, the phenomenon has not so far been observed in the genus *Nais*. In advanced stages of maturity the mouth becomes closed; the buccal cavity and anterior part of the pharynx lose their lumen and become reduced in size; the pharyngeal cells lose their distinctness of outline, and those of the ventral wall are reduced in size, low and cubical. Behind the pharynx the gut is continued as a narrow band without a lumen as far as segment xii.; the cells lose their regular epithelial arrangement, and the solid cord is, seen in section, smaller than, or sometimes about the same size as, the ventral nerve-cord; there may be small spaces here and there, filled with fluid; there are large blood-vessels around it, in close contact with it. Behind the sperm-sac there are small cavities in the solid cord of disintegrating cells; but after segment xvii. the intestine, though still narrower than in the normal worm, retains its proper form, and is lined with columnar cells surrounded by chloragogen cells; the lumen is either empty or contains some granular matter. Although the gut is thus degenerating in the anterior part of the body, the nephridia are normal, the blood-vessels are larger than usual, and the same is the case with the cerebral ganglion; the specimens manifested the characteristic wriggling movements, and were thus in no way pathological.

When such specimens were kept under observation for three days, their anterior portions, containing the genital organs, separated off as a sort of cocoon, while the hinder part of the animal lived for some time, but was unable to regenerate and ultimately died. It appears, then, that death ensues after the full attainment of the sexual phase, and the cocoon is probably the whole anterior region of the worm which has been separated off.

BRANCHIODRILUS HORTENSIS Stephenson.

Many examples of this species were collected during the last two weeks of October and the first two weeks of November, from the mud at the bottom of a pond at Sikandra; and of these nine were found to possess fully developed sexual organs (text-fig. 3).

Text-figure 3.



Genital region of *Branchiodrilus hortensis*. The atria lie one on each side of the sperm-sac, and the vas deferens is seen running internal to the atrium of its side; the funnel lies far behind in the sperm-sac. *Pr.*, prostate; the remaining letters as before. × ca. 125.

The clitellum occupies segments v.–viii.; it is opaque white in the living animal. It is about ·05 mm. thick; the cells have a coarse reticular structure, the meshes of the network being clear spaces; the nuclei are indistinct. The clitellum is absent between the spermathecal openings and on the ventral surface in the anterior portion of segment v. It is formed after all the other sexual organs have been developed.

The testes had disappeared in all the specimens examined.

The sperm-sac may reach as far back as segment xix. or xx., in two cases to xxvi.; usually it extended to xviii.

The male funnels are within the sperm-sac, some distance behind its mouth, and here they nearly fill up the available space. Their lips are everted, and their outer margin is attached to the wall of the sperm-sac. The width of the funnel is 90 μ; its cells are high and ciliated, with nuclei at their base. The cells and cilia of the upper lip seem to be taller than those of the lower.

The vas deferens is 30 μ in diameter; it is a fairly long tube, about ·2 mm. in length, and consists of two parts, a posterior longitudinal and an anterior ascending portion. The longitudinal portion passes forwards from the funnel, and is about 165 μ in length; its last part lies over the upper wall of the sperm-sac. The tube then bends upwards; the vertical ascending portion, about 90 μ in length, lies just behind septum 5/6. In a few specimens the longitudinal portion formed a distinct curve towards the ventral body-wall before rising to be continued into the ascending portion. The cells lining the vas deferens are about half as high as those of the funnel, have oval nuclei at the base, and are without distinct cell-outlines; there is a thin covering of muscle-fibres outside the epithelium. The tube enters the atrium on its anterior face much above the middle; the ascending part of the duct as it opens into the atrium is surrounded by a thick coat of muscle-fibres, continued onto it from the muscular covering of the atrium; the change from the cubical cells of the duct to the columnar cells of the atrium is sudden.

A bundle of muscle-fibres directed upwards from the ventral body-wall is attached to the ascending portion; and a few fibres connect it above to the dorsal body-wall behind septum 5/6.

The atrium is a large pear-shaped body, taking up nearly the whole length of its segment, 230–240 μ in height and about 190 μ in length antero-posteriorly; in only one specimen were spermatozoa seen in its interior. The epithelium is columnar, the cells 18 μ by 15 μ, with oval nuclei lying at the base; outside the epithelium is a thick coat of circular muscular fibres.

The ejaculatory duct, about 78 μ in length, opens at the top of a tubular depression of the ventral body-wall about 42 μ in depth, and is capable of being everted, when it projects slightly as a short pseudo-penis. The epithelium of the duct consists of columnar cells with elongated nuclei, and has a thick investment of muscle-fibres.

The "prostate" consists of a large mass of pear-shaped cells around the ejaculatory duct; the cells contain granular protoplasm and a large oval or rounded nucleus near the base. A few muscle-fibres surround and enter the mass of cells from the ventral body-wall. There are a few blood-vessels around the atrium and prostatic cells. Two bands of muscle-fibres, arising from the setal sac, are attached to the atrium behind. The male opening lies internal to and at the level of the ventral setæ about the middle of segment vi.

The ovisac, formed by the backward bulging of septum 6/7, and, as usual, enveloping the sperm-sac, is filled with a large mass of spherical and elliptical yolk granules about 7–15 μ in diameter. The ova are fairly large, and lie in two or three masses.

The female funnel, about 45 μ in height, lies over the lower portion of septum 6/7 near the ventral parietes in segment vi. No female opening was seen.

The large spermathecæ occupy the fifth segment. The ampulla is somewhat heart-shaped, or ovoid and notched below where the duct arises. Its size varies somewhat: in height it may be from 207 to 270 μ, its length antero-posteriorly rather greater and its width rather less. The ampullæ are filled with spermatozoa, and are so large as nearly to fill up the whole segment, the remaining organs occupying only a small space below their contiguous inner walls. The part of the ampulla anterior to the duct is somewhat bulged downwards, and is lined with columnar cells; the part of the wall behind the duct is lined with cubical cells, which gradually decrease in height as they pass upwards on the posterior wall; the rest of the ampulla is lined by a very thin epithelium of attenuated cells whose outline is quite indistinct. Outside the epithelium there is a thin coat of circular muscular fibres—the only part of the wall visible over a large portion, on account of the thinness of the epithelium. The spermathecal duct leaves the ampulla below, nearer its anterior wall, and is about 130–140 μ in height, including the depression of the body-wall where it opens to the exterior. The duct is narrow above and below, but somewhat swollen in the middle; its epithelium consists of narrow columnar cells having elongated nuclei. There is a thick covering of muscle-fibres outside the epithelium. The spermathecal opening lies internal to and at the level of the ventral setæ of the fifth segment, some distance behind septum 4/5.

The penial setæ are the modified ventral setæ of segment vi. They are two or three in a bundle, somewhat hooked at the distal end, which is not bifid. In length they are about 132 μ; the shaft consists of a distal narrow portion about 36 μ long, and a proximal stouter part 96 μ long; there is no distinct nodulus, but the distal narrow portion is bent outwards and thus not in a straight line with the proximal segment (text-fig. 1).

References to Literature.

1. BEDDARD, F. E.—"A New Branchiate Oligochæte (*Branchiura sowerbyi*)." Quart. Journ. Micr. Sci. vol. xxxiii., 1892.
2. STEPHENSON, J.—"On *Branchiura sowerbyi* Beddard, and on a new Species of *Limnodrilus* with distinctive characters." Trans. Roy. Soc. Edin. vol. xlviii. pt. 2, 1912.
3. STEPHENSON, J.—"On the Sexual Phase in certain of the Naididæ." *Ibid.* vol. li. pt. 4, 1915.
4. STEPHENSON, J.—"On *Hæmonais laurentii*, sp. n., a representative of a little-known Genus of Naididæ." *Ibid.* vol. li. pt. 4, 1915.

29. Observations on the Flight of Flying-Fishes.

By E. H. Hankin, M.A., Sc.D., Agra, India*.

[Received August 4, 1920: Read October 19, 1920.]

(Text-figures 1 & 2.)

A point hitherto overlooked in the study of the flight of flying-fishes is that the air is suitable for their flight to very different degrees on different occasions. In this respect their flight resembles that of soaring birds. This statement may be illustrated by the following examples.

1. *Flight under unsuitable atmospheric conditions.*

On the 1st June, 1920, at about a quarter of an hour after sunset, the ship on which I was travelling across the Arabian Sea was disturbing groups of small flying-fishes at the rate of one or two groups per minute. The surface of the sea was either glassy or disturbed by ripples too small to be easily visible.

Each fish, on emerging, jumped out of the water so far that, while the body was supported on the outstretched "wings," the end of the tail was still immersed. This organ was thereupon wagged vigorously from side to side, as is usual when starting, thus forming a trail of ripples in the water. After proceeding thus for the unusually long distance of four or five metres, the fish raised its tail from the water and began to glide. The length of the glide made by each fish was, at first, about a metre. Within a few minutes a change was observed. The fishes of each group disturbed by the ship made shorter and shorter glides, until at length each fish fell into the water immediately it ceased to move its tail.

One fish flapped its wings at starting, but made no better glide than the others.

About half an hour previously, in sunshine, the ship had also been disturbing small flying-fishes, which had flown for such distances as are usual. Just before sunset the first symptoms of lessened suitability of the air for their flight were observed. The fishes began to show lateral instability. It may be noted that both vultures and flying-fishes are more apt to show lateral instability late in the afternoon than at other times of the day. The stage of lateral instability shown by the flying-fishes soon passed off and was replaced by one in which the course of each fish, instead of being a horizontal straight line, was undulating. Each fish showed two or three alternations of gain and loss of height before falling into the water. This condition soon changed to that first described.

---

* Communicated by C. Tate Regan, F.R.S., F.Z.S.

In view of these gradual changes in the performances of the fishes, there seems to be no room for doubt that they wished to get away from the neighbourhood of the ship, by air and as quickly as possible, throughout, and that the air was getting progressively less and less fitted for their flight.

On the other hand, it has been observed by me on many occasions that the air remains suitable for the gliding flight of flying-fishes after sunset if wind is present.

2. *Flight under fully favourable atmospheric conditions.*

During the same voyage, in sunshine and in the presence of a light wind, flying-fishes were seen by me to fly at a uniform height above the water till they were out of sight. This was noted on two or three occasions. On a previous voyage I had seen a flight till out of sight under cloud in a monsoon wind. A binocular was used for these observations. Usually the longer flights appear to be between 200 and 400 metres in length. In a flight of this kind the following phenomena may be noticed:—

The fore wings (pectoral fins) are usually in the "flat" position, *i. e.* extended in the horizontal plane. Sometimes the wings are slightly inclined upwards. In this case the outer part of the wing is at a higher level than its base. This may be called the "up" position. Rarely the wings are inclined very slightly downwards. This may be described as the "down" position. This latter disposition, which I was only able to see distinctly on my recent voyage, is probably that used for flight at highest speed, as in slow-speed flight the wings are inclined upwards to a strong degree.

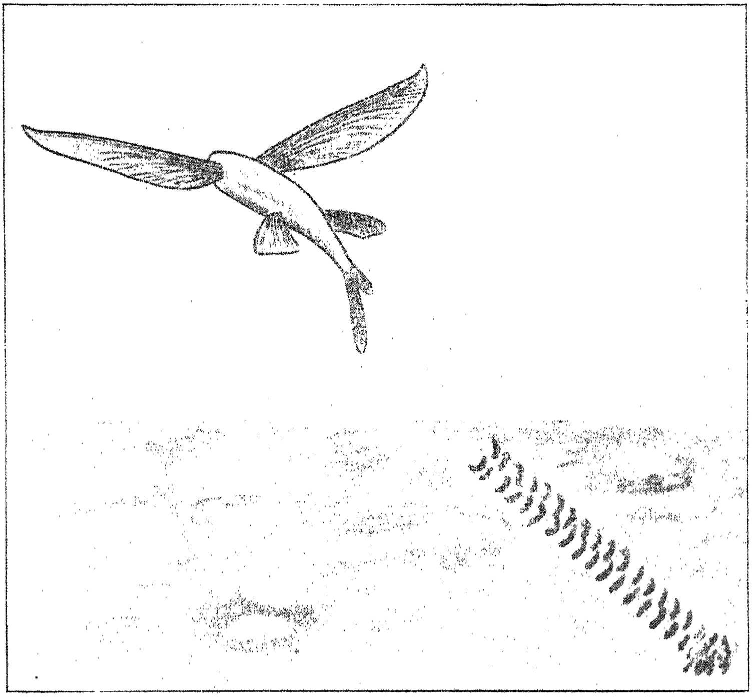
Thus in respect of its wing-disposition the flying-fish resembles the soaring vulture, for vultures have their wings in the "up" position for slow-speed flight and use the "flat" wing disposition for flight at high speed. A further resemblance is indicated by the following very unexpected observation:—

If the flying-fish is very carefully observed the extreme wing-tips, for nearly an inch of their length, may be seen to be bent up forming an angle of perhaps 45 degrees with the rest of the wing. If the sun is not far above the horizon, and if the fish is travelling away from the observer in a southerly (presumably also in a northerly) direction, then the wing-tip furthest from the sun appears thicker than the other. This appearance has been seen by me quite clearly and definitely in flying-fishes of two different species. The appearance seems to be due to the upturned wing-tip being bent round so that it has a negative angle of incidence and hence, when the sun is low, the underside of one wing-tip is seen in shadow. When the sun gets higher the visibility of each wing-tip is reinforced by shadow in this way. But, at best, the upturned wing-tip is by no means easy to see.

The bent-up wing-tips show no appearance of vibration. They appear as if held in their position by a steady force. As I have stated elsewhere ('Animal Flight,' Iliffe and Sons, 1914), the wing-tips of vultures in horizontal soaring flight show the terminal quills bent up as though they were under the influence of a steady force acting from below and behind.

As the fish is emerging from the water an interesting appearance may sometimes be seen. The length of the trail (made by lateral movement of the tail) is generally less than a metre and a half. It may be only half a metre. At the end of the trail in a few observations the fish appeared to make a sudden jump out of the water, gaining height thereby to the extent of four or five inches. Had this appearance of a jump been due to an extra strong stroke by the tail, one would have expected to have seen an extra large ripple in the water. Nothing of the kind was observed. On other occasions, when the jump was not seen and, I believe, did not occur, the trail was observed to get fainter towards its end (text-fig. 1).

Text-figure 1.



Flying-fish starting, showing trail of ripples made by movement of tail. Wings up and tail down as in slow-speed flight.

3. *Speed of flight of flying-fishes.*

During my recent voyage a flying-fish was seen flying on a course parallel with the ship and at the same apparent speed. During eight seconds, timed with a stop-watch, it remained fixed in position relatively to the ship. The latter was travelling through the water at 15½ knots or 7¾ metres per second. The direction of the real wind was learnt by noting the movement of the waves, that of the apparent wind by the position of the line of smoke from the funnel. From these data it was calculated that the velocity of the wind was 4 metres per second and that of the flying-fish through the air was 10 metres per second. This estimate involves the assumption that the wind-velocity was the same near water-level as at the level of the top of the funnel.

A similar observation on another flying-fish gave an identical result. Later in the day the wind decreased, and then flying-fishes travelling on the same course as the ship were seen to move distinctly faster than the latter.

These flying-fishes were all gliding with tails hanging down and wings "up." That is to say they were in slow-speed flight. In 'Animal Flight' reasons have been brought forward for believing that, when in high-speed flight (wings flat and tail up on a level with the body), flying-fishes may attain speeds of more than 20 metres per second.

Flapping sometimes occurs at starting, especially in the presence of wind and in the colder months of the year. The above-described observations of the position of the wing-tips, and also the sharp-cut appearance of the wings in species whose wings are opaque, definitely prove that flapping does not occur when once the fish is well under way. Hence flapping cannot be invoked as an explanation of the speed maintained during flight.

Sometimes—when it may be supposed that the air is not fully suitable for flight, or perhaps if the fish is exceptionally frightened by the ship—during its flight the fish lowers its tail into the water at intervals of about two seconds and wags it to and fro for a fraction of a second with a resulting increase of speed.

4. *Comparison with the speeds attained by vultures in horizontal soaring flight.*

That the speed of flight of flying-fishes is similar to that of soaring vultures when in horizontal flight is shown by the following figures:—

During April 1920, I made several measurements, in Agra, of the apparent speed of vultures with the help of a Souchier telemetre by the method described by me in 'Animal Flight.' Information as to the velocity of the wind in which the vultures were gliding was obtained from measurements made with the help of balloons sent up by Mr. J. H. Field (to whom I owe my thanks) from the Agra Aerological Laboratory. The balloons were sent up at the time I was making my measurements. On one day seven balloons were let off while I was observing. From data thus obtained, it was possible to deduce the speed of the vultures through the air.

Another set of measurements were made by me during the first eight months of the year 1915. In these cases, however, the balloons had been liberated four or five hours before my observations were made. An error is thus introduced into the calculations which, it may be noted, is likely to be less on days of light wind than in stronger winds.

The results of these two sets of observations agree in indicating that vultures soar at higher speeds in stronger winds. The mean speeds calculated from my data are as follows:—

	Observations made in	
	April 1920.	January to August 1915.
Velocities of wind, in which the vultures were flying. in metres per second.	Mean speed of vultures, in metres per second.	
0–3	11·6	11·7
4–6	11·8	14·1
7–9	15·0	17·2
10–20	20·0	17·7

The above figures are based on 122 observations made in April 1920 and 696 observations made in 1915.

Reasons have been adduced by me for believing that the vultures on which the above measurements were made, were, as they appeared to be, actually in horizontal flight and that their speed, which they can maintain indefinitely, cannot be explained by loss of height. An additional reason may here be mentioned for this belief. It is that if a vulture glides, in soarable air, with even a small loss of height, its speed will very greatly increase beyond the above figures. For instance, in April last a measurement was made of a speed of 42 metres per second in a vulture flying nearly with the wind. The wind had a velocity of only 2½ metres per second at the height at which the vulture was flying. Hence the speed of the bird through the air must have been about 40½ metres per second. As this speed was exceptional and as the bird was travelling in the direction of a place where vultures frequently settle, it was assumed that it was gliding with loss of height, though no loss of height was seen, and it was not included in the calculation of the mean speeds above given.

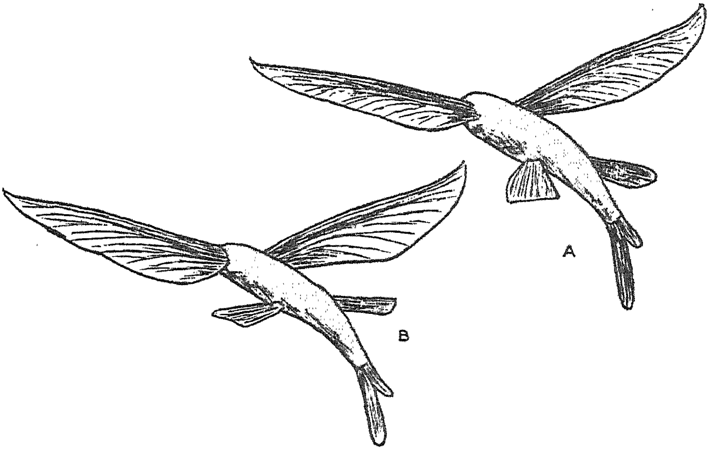
If vultures in soaring flight attain velocities of ten to twenty metres per second and if their velocities tend to increase as soon as they begin to glide downwards, it is obvious that they must possess some means of checking speed. Otherwise they would be unable to land without accident. In 'Animal Flight' two methods of checking speed, one used for high-speed flight, the other used for low-speed flight, have been described. Two analogous methods, for slow and fast speed respectively, employed by flying-fishes have now to be described.

5. *Method of checking speed in high-speed flight.*

This method, which depends on changes of position of the hind wings (pelvic fins), has only been followed by me in species whose wings are coloured. It would be quite beyond my powers of observation to see the adjustment in those species whose wings are more or less transparent. Of the species that have yielded most opportunities for these observations may be mentioned one with black hind wings and another whose hind wings have a chocolate-brown colour. The observations about to be described are very difficult to make, and the following account is, to some extent, compiled from glimpses of parts of the adjustment seen on different occasions.

The flying-fish starts its flight with the hind wings directed outwards and backwards and extended in the horizontal plane. At some distance, perhaps 50 metres, from the end of its flight, it may be seen suddenly to lower its hind wings (pelvic fins) so that they point nearly vertically downwards. On my recent voyage, when using a binocular of magnification 10, it appeared to me that, when the hind wings are in the down position, their plane is parallel to the direction of flight. In this position the leading edge only of the hind wing would offer direct resistance to speed ahead. But on a voyage in 1914, when I was using an Aitchison binocular of the very unusual magnification 25, on two occasions the hind wings, when in the down position, appeared to me to be slightly rotated round their long axis so that their hind margins approached each other. On one of these occasions, during part of the flight, one hind wing was less visible than the other. This was probably due to its having been seen end on. When the fish changed its course so that it was travelling directly away from me the two hind wings became equally visible. With the hind wings thus disposed it is obvious that the air passing between them must be, so to speak, entering a funnel, and therefore much resistance would be offered to speed ahead. It is probable that these two dispositions of the hind wings are used successively, for, within about a second of the end of the flight, the two hind wings are suddenly rotated through nearly a right angle round their long axes. The result of this manœuvre is that the plane of the hind wings acquires a position at right angles to the direction of flight. In the first down position the hind wings are not fully expanded. In the last position they are expanded to their greatest extent, thus offering the maximum resistance to speed ahead. On one occasion the adjacent edges of the two hind wings appeared to me to overlap. Almost or quite simultaneously with the full rotation of the hind wings, the tail is lowered and the fore wings are placed in the up position. The tail then touches the water, and the fish falls in with practically no splash.

Text-figure 2.



A. Flying-fish in low-speed flight.
B. Hind wings advanced at end of flight.

In monsoon winds the fish may place its hind wings in the down position and even rotate them almost from the commencement of its flight. If this is done no high apparent speed is attained even in cases in which the fish is travelling at right angles to the wind.

Much practice in observing flying-fishes was needed by me before it was possible to see these adjustments of the hind wings. On my last voyage, in June 1920, I was able to see clearly the full rotation of the hind wings in flying-fishes of three different species.

6. *Method of checking speed in slow-speed flight.*

If the flying-fish is making a flight at slow speed, as happens more frequently in the colder than in the hotter months of the year, and as happens usually in the absence of wind, an entirely different means of checking speed is employed and one which is much more easy to observe.

During slow flight the fore wings are strongly inclined up and the tail hangs down. The hind wings, as in high-speed flight, are directed outwards and backwards. Towards the end of the flight the hind wings are somewhat suddenly advanced (text-fig. 2). They still remain extended in the horizontal plane. The effect of this movement is to bring the lift of the wings as a whole further forward in respect of the centre of gravity. The fish consequently rotates round its transverse axis. It is a rotation upwards, *i. e.* the head goes up, the tail down. The angle of incidence of the fore wings is consequently increased to such an extent that their plane assumes a large angle with the direction of flight. Consequently they present great resistance to speed ahead. The speed rapidly decreases and the fish drops. The tail is the first part to be immersed, and the animal falls in with a very small amount of splash.

7. *Termination of flight without checking speed.*

A species of flying-fish is known to me which is of small size and which generally appears in groups of eight or ten individuals. They do not, as a rule at least, fly either so far or apparently so fast as individuals of other species that have come under my notice. Their flight also differs in two other respects. First, they usually fly in a straight line and do not follow the water-surface as is generally the habit with other species. Secondly, at the end of their flight they steer downwards by retiring the wings through an angle of about forty-five degrees. They then plunge head foremost into the water without any visible attempt to check their speed.

It is possible that this species is identical with *Exocœtus evolans*. This is the name of a species, or of a group of closely allied species, which differ from other flying-fishes in that their pelvic fins are small and placed far forward. Hence these fins are unfitted to function either for checking speed or for steering in the vertical plane.

It is probable that the frequent shortness of the flights of flying-fishes is often involuntary. My observations indicate that flying-fishes sometimes behave as if they had made a mistaken estimate of the suitability of the air for their flight. On one occasion I noticed that they were starting with their wings disposed for slow-speed flight, that they immediately changed over to the high-speed disposition and then, at once, fell into the water with a splash. On my recent voyage I noted, on one occasion, that flying-fishes were starting with tails up (*i. e.* as in high-speed flight). They then, either at once fell into the water or lowered their tails and flew on. On other occasions when groups of small individuals emerged they all at once fell in with splashing or, in some cases, while the rest splashed in, one or two got away and made flights of normal length.

30. Observations on the Life-History, Biology, and Genetics of the Lady-bird Beetle, *Adalia bipunctata* (Mulsant).

By Onèra A. Merritt Hawkes, M.Sc. (Birm.), B.Sc. (Lond.) *.

[Received July 3, 1920: Read November 2, 1920.]

Contents.

	Page
1. Introduction	475
2. The Food and Feeding of *Adalia bipunctata*	477
3. Notes on the Life-History	480
a. Mating	480
b. The Eggs	481
c. The Larvæ	482
d. The Pupæ	482
e. The Imagines	483
f. The Enemies of the Lady-bird	483
g. Hibernation	484
4. The Genetical Relations of the Varieties	485
5. Summary	488

1. *Introduction.*

During three years of breeding pure and hybrid silkworms (*Philosamia*), I have been increasingly impressed by the apparent reasonableness of what would be regarded as fluctuating varieties: and by reasonableness, I mean a genetic relation between the variations of the parents and those of the offspring. To understand such variations, what appears to be needed is a large number of exhaustive studies of normally occurring varieties in animals untouched by Man. Insects present a large number of variations, but little or nothing is known of their inheritance. The Japanese have made extensive studies of silkworms (largely domesticated), and in America, Roswell Johnson (**13**) has made a wide study of *Hippodamia*, as a result of which he has been able to make the following important statement (**13**):—"Every variety or noticeable variation of *Hippodamia* that has been tested is inheritable in some degree." Miriam Palmer (**21**, **21** *a*) has also made successful studies of the American varieties of *Adalia* and other Coccinellids. Meissner (**19**, **20**) and Schröder (**23**), in Germany, have made a small number of breeding experiments with some of the varieties of *Adalia bipunctata*.

Work of this kind would have the added advantage that in some cases the sciences of genetics and classification would be able to go hand in hand, instead of, as is too usual, being mere bowing acquaintances.

Adalia is highly suitable for work of this character, as there

---

* Communicated by E. Green, F.Z.S., F.E.S.

are many easily procurable varieties, which, as far as is known, are not regional.

Palmer (**21**) worked for some time at *Adalia*, but she had only a few varieties to deal with, as in America there occurs only the "type" and three varieties, whilst in Europe there are more than twenty-six named varieties. It would be impossible to get as quick results here as in America, as two generations per annum are the most one can obtain in England under natural conditions, whereas Palmer succeeded in obtaining four and five during the long American summer. Our erratic climate also makes the food-supply (aphides) more uncertain than under more stable climatic conditions.

Coccinellids have been extensively studied in the United States, as they are there recognised to be of considerable economic importance; but in England there has been little careful study of their habits, their distribution, or the genetical and possibly regional relations of the varieties which are so numerous in some of the species. Donisthorpe (**6**) has published the only complete history of any species, *Coccinella distincta*. The following observations were made in the course of genetical experiments which are still in progress.

The varieties of *Adalia* have been determined chiefly by Meissner and Schröder, who based their determination principally upon the variations in the colour of the elytra, but neglected the very considerable variations of the thorax. Schröder believes that the varieties from pure red elytra at the one extreme to pure black at the other are modifications of a scheme of seven spots and a scutellar mark. This is an interesting matter of speculation, but we do know that in Europe there are two principal forms: (1) "type," in which the elytra are a reddish brown with an approximately round black spot in the middle of each elytron; and (2) a black form with either two or three red spots in each elytron: when two are present, an upper lateral and a mid-dorsal, the variety is known as var. 4-*maculata*; when three are present, an anal red spot being added to the above two, the variety is named 6-*pustulata*. All other varieties, none of which occur in large numbers, can probably be grouped about these two main forms.

The Red varieties are generally acknowledged to be commoner than the Black, though very few accurate statistics have been recorded. Meissner found 35·2 per cent. Black in Summerfeld and 42·3 in Potsdam. In Staffordshire and Warwickshire I found 29 per cent. Black in 1918, 25 per cent. in 1919. In 1920 I found 2·75 per cent. Black at Crouch Hill, London, N., 42·7 per cent. Black on hops at Bishop's Frome, Herefordshire, 11·7 per cent. at Enville, Staffordshire, and, very much to my surprise, 78·5 per cent. Black in the Edgbaston district of Birmingham. Further observations will show whether localities are characterised by certain varieties or whether the prevalent varieties vary from time to time. If the varieties remain the same, will it mean that there is little or no migration, that hibernation takes place locally, and that the varieties breed true? Or, does the particular environment allow only certain varieties to survive?

Two, possibly four, factors have to be considered in a genetic study of the Black and Red forms:—

1. Pattern: that is, the shape and distribution of the spots.
2. Colour: (*a*) black, which is the same in both "type" and black varieties;
   (*b*) red, which, contrary to accepted opinion, I believe different in the Red and Black forms.
3. Size: there is great range in size in the Coccinellidæ, which Johnson believes is chiefly adaptational, but the mean size of the varieties under consideration is different, and perhaps constitutes a definite character.
4. There may be a physiological factor in the reaction of these varieties to heat.

Microscopical examination by transmitted light shows that the reddish colour in both varieties is due to a clear yellow, to which brownish-red, semi-transparent particles are added in the Red form and red-brown and carmine in the Black variety.

There is probably a physiological factor to account for the seasonal appearances of the two forms, in England the Black usually appearing later and disappearing earlier than the Red. I have also observed that when the breeding-boxes were overheated, the Black could live at a higher temperature than the Red.

2. *The Food and Feeding of* Adalia bipunctata.

There is considerable difficulty in feeding *Adalia* with its food, living aphis. The occurrence of aphis is very erratic, being much affected by sudden climatic changes, such as cold, wind, and heavy rains. At times they disappear inexplicably.

Adalia will eat many but not all species of aphis. During two years' breeding I have found three species which are not acceptable:—(1) *Aphis rumicis*, the black bean aphis which is found on broad beans in early summer. The young of this species are eaten to a small extent, but the large only under stress of circumstances. One may continually find a bean-row black with this destructive aphid, but very few lady-birds upon them when, on a bed of nettles a few yards away, can be found large numbers of Coccinellidæ—*C. septempunctata*, *C. variabilis*, *A. bipunctata*, *Halyzia* 14-*guttata*, *H.* 22-*punctata*, and *H.* 14-*punctata*,—even when the aphids are not obviously numerous. (2) A bluish-green aphis (*Macrosiphum aconitum* (Van der Goot)), which I have found only on Monkshood. This has never been eaten by *Adalia*. Johnson says "several of the highly-coloured aphis cannot be successfully fed to Coccinellids." (3) *Hyalopterus pruni*: this aphis has a grey-green mealy exudation, which fills the stomata of the larvæ and so kills them. When a Victoria plum was covered with this aphis, no larvæ or imagines were ever found among them, and very few larvæ of the Hover-fly, which is probably an even more prolific eater of aphis than the Coccinellidæ.

The presence of large numbers of Coccinellidæ on the Stinging Nettle may be due to the fact that these insects are not universally carnivorous. *C. septempunctata* certainly eats the abundant pollen and possibly other products of this plant. Donisthorpe found that *C. distincta* ate the honey supplied to ants, and I have found *C. septempunctata* eat the exudation from bean plants and Jerusalem artichokes in the autumn. During the summer I have observed *A. bipunctata* apparently eating the juice of raspberries and split plums.

The *Adalia* larvæ in the first two instars have to be fed with minute aphis, as, although sufficiently pugnacious to attack large aphis, the latter can easily shake them off.

Any species of aphis were used in 1918, but in 1919 practically two species only—in early summer *Aphis pruni* Fab., which attacks damson-trees; and for the remainder of the year *Aphis fagi*, which lives only on the beech. Although the latter is slightly woolly when full grown, it is in the earlier stages very acceptable to *bipunctata*. The copper-beech is attacked more frequently than the green beech, and on the former numbers of *bipunctata* are to be found all the summer. The supply of beech aphis has the advantage of being fairly constant, as the leaves and branches are so flat and so close together that it takes a great deal of cold and rain to clean the aphis off the tree. The flat leaves, which do not wither readily, are very suitable in boxes. The aphis of the rose (*Siphonora rosæ*) and of the nettle (*Aphis urticia*) both die quickly in boxes, presumably owing to the wilting of the thin leaves of the food-plants.

In August 1920, after a variety of experiments, I found that the adults will eagerly eat pounded dates, upon which they can live for months. The newly hatched larvæ cannot use this food at all, but I succeeded in bringing one larva from the second instar to the perfect insect on dates alone, the imago being of average size. Most of the older larvæ kept alive on this diet for some time, but did not grow much and ultimately died.

I have obtained the best results by feeding in closed boxes. The boxes must be opened every day, not only to introduce fresh food but also fresh air, which is of paramount importance to this species. Great care has also to be taken to remove all mouldy leaves. A mould (probably *Cladosporium aphidis* Jhüm) quickly grows on the honey-dew produced by the aphis, especially that found on beech and sycamore leaves. This mould fatally attacks the larvæ. It first appears on the thorax, but its method of producing death is undetermined.

The main difficulty of rearing is the cannibalistic habit of not only *A. bipunctata*, but also *C. septempunctata*, *C. variabilis*, and *H. 14-punctata*. The larvæ eat eggs and one another in either the larval or pupal stages. This phenomenon is not due to confinement or lack of food, as it takes place in the presence of abundant food and in normal natural conditions. One can easily watch what appears to be a form of Coccinellid degeneracy among the larvæ which frequent red and black currant bushes. I have seen adult *bipunctata* and *septempunctata* eat their own eggs in boxes and on the trunks of trees, but never eat either larvæ or pupæ. This habit was also observed (**6**) in *C. distincta* in confinement. Palmer has, however, observed the imagines eating larvæ when there was no other food in the cages. On one occasion I watched a *bipunctata* eat the abdomen of a small fly caught in a spider's web. After a period of experimental starvation, two *Adalia bipunctata* feasted upon a small weak relation. Cannibalism has also been noticed by Palmer, Johnson, Burgess, etc.

On hatching, the almost colourless larvæ remain clinging to the empty egg-shells, part (never all) of which forms their first meal. They next fall upon one another. This same early habit of cannibalism also occurs in *Epilachna* (**27**), the vegetarian Lady-bird. If by chance an egg lags behind the others, it never hatches, for it is eaten by a larva which was born a little earlier. The larvæ remain on the egg-mass until fully coloured, and then suddenly and simultaneously disperse. Approximately a quarter of the larvæ are eaten before this dispersal.

During the first instar there is great mortality, partly owing to lack of sufficiently small aphis and partly to cannibalism. The young larvæ do best in small boxes, as they seem incapable of wandering far at this stage to find food, which, I believe, is chiefly obtained by good luck and persistent wandering. As early as possible the larvæ were isolated in separate boxes, but I was inclined to think cannibalism in the early stages a physiologically highly suitable diet, and, with this in view, I fed the *bipunctata* with small larvæ of other species. This practice was not, however, always successful, as sometimes the eater became the eaten. Partially successful attempts were made to feed the larvæ on cooked and raw hen's egg. Coccinellid eggs were always eaten when put in the boxes, but this is not a suitable proceeding in the early instars, as an odd egg may escape and hatch. During 1918, 21 of 22 families were reduced to one, as the full significance of cannibalism was not then recognised.

It is interesting to consider the intermittent competition between larvæ of the same batch of eggs. It is not the larva which first starts in the race which necessarily first reaches the winning-post. It may be the first to reach the end of the first instar, but during the short quiescent period which precedes ecdysis, it becomes a defenceless prey to those who have lagged behind. This special danger recurs at the end of each of the four instars.

The method of attacking the pupa is always the same, the larva beginning on the ventral side near the anal point of attachment and eating its way upwards and forwards, half burying itself in the process. The head, the thorax, and the tough dorsal skin are frequently left untouched.

There is, however, no special mode of attacking the aphis, and certainly no painless method of dining. The *bipunctata* catches hold of a passing aphis and at once proceeds to devour it in spite of its struggles, which continue far into the meal. The legs, the wings, the head, and part of the cuticle of abdomen and thorax are usually left. The meal may take as long as five minutes.

The mother *bipunctata* is not very wise in her choice of a position for her eggs—many are laid on leaves, but also many on the branches and trunks of trees. I have even found them on wooden palings and on stones by the side of garden-paths. As the young larvæ cannot wander far in search of food, and as the parent is lacking in the instinct to lay eggs where there would be an adequate larder, the capacity for eating eggs and one another may be of considerable biological value. Indeed, knowing what we do of aphis, one realises that it would indeed be a wise Lady-bird that could guarantee aphis for its newly-hatched young. The period of incubation varies from three to nine days, and in that time the aphis might have disappeared. In May 1918 the damson-trees were covered with aphis for three weeks; without any apparent change in the weather, the aphis began suddenly to descend the tree-trunks in myriads, and at the end of two days hardly an aphis could be found. I have found eggs laid on the petals of a rose, but the petals fell before the eggs hatched.

The use of cannibalism was well demonstrated in July 1920. An isolated gooseberry-bush had every shoot attacked by aphis, upon which large numbers of *bipunctata* larvæ were feeding. At the time when the larvæ were beginning to pupate, a few cold rainy days caused the aphis to completely disappear. At once the larvæ began to attack each other and the pupæ, and, finally, themselves pupated on an entirely cannibal diet. I saw no signs of migration from this bush on account of shortage of aphis.

Cannibalism is probably of use in preserving the race during periods of aphis famine, as the larvæ, unlike the adults, cannot live long without food. Cannibalism is not of the same biological use to the imago, as its power of flight gives it a large range, and, when necessary, it can remain long periods without food. I have starved Lady-birds for three weeks, and at the end some of the males were capable of successful fertilization.

3. *Notes on the Life-History.*

a. *Mating.*

Mating takes place in captivity in the presence of plenty of light, especially direct sunlight. The response to light is very rapid. Immediately a box containing a number of Lady-birds is put in the sunlight, they begin to move quickly, fly, and mate. The same activity does not take place if the box is warmed without light. Fresh air, especially moving air, is also conducive to mating.

A. bipunctata is both polyandrous and polygamous. When a male and female are isolated in a box, mating takes place at intervals during a period of two to nine weeks. Copulation lasts from half to three-quarters of an hour. It takes place when no eggs are laid and when the egg-laying period of the female is finished. Palmer states that the female lays fertile eggs three weeks after fertilization. Mating takes place in Staffordshire and Warwickshire during the whole summer, but the principal season is May to June, with a subsidiary season from the middle to the end of August. Probably only a very few of the newly emerged Lady-birds breed until the following year. The insects have been found mating on sunny days in late September, but at that time no eggs were laid.

b. *The Eggs.*

TABLE I.

Detailed Record of Family, 33 (1919).

Dates of Oviposition.	Number of Eggs and Colour.	Incubation. (Days.)	Larval life. (Days.)	Pupation. (Days.)	Number of Imagines.
(1) 22. 7. 19	16 (yellow)	5	25	8	6
(2) 22. 7. 19	24 (orange)				
(3) 23. 7. 19	8 (deep orange).	9	16	7	1
(4) 27. 7. 19	8 (,, ,,).	6	—	—	—
(5) 27. 7. 19	11 (,, ,,).	6	17	13	3
(6) 27. 7. 19	3 (yellow base, orange tip).	6	24	7	1
(7) 28. 7. 19	21 (orange).	7	17	8	2
(8) 29. 7. 19	25 (yellow base, orange tip).	5	22	9	1
(9) 1. 8. 19	25 (deep orange).	—	—	—	—
(10) 3. 8. 19	24 (,, ,,).	6	19	—	—
(11) 7. 8. 19	12 (,, ,,).	3	18	7	9
(12) 9. 8. 19	8 (,, ,,).	3	24	7	1
	Total 185	Av. 5·6	Av. 20·2	Av. 8·2	Total 24

Mating took place on 17.7.19 between two Red "type" *Adalias*. In batches (1) and (8) the larvæ had light rings around all the abdominal and thoracic tubercles: hence these larvæ appeared much lighter than the larvæ of the remaining batches, which only had light rings around the lower lateral tubercles. The resulting imagines were all red, those from these two batches being indistinguishable from the others.

The eggs are spindle-shaped and laid in batches of from three to fifty. The outer shell is colourless and covered with numerous protuberances. The colour of the egg is due to the yolk, which is usually yellow but may be orange—a range of shades similar to those of the yolk of the hen's egg. Usually the whole batch of eggs laid on a single occasion is of the same uniform colour, but they may vary (see Table I.). In several batches the eggs shaded from yellow at one end to orange at the other. The eggs do not change in colour until a few hours before the larvæ are to merge, when they become a greenish grey.

The average number of eggs laid was between 140 and 148, the largest numbers laid were 167 in 1918, 189 in 1919, and 418 in 1920. The largest number laid in twenty-four hours was 80. The Black and Red forms are not differentiated by the colour, size, or shape of the eggs or by the number of eggs laid. Clausen (**3**) found 190 the average number laid in America.

The eggs are usually laid on the under side of leaves, but may also be found in slight depressions on the trunk and branches; on the trunk they are usually on the north side or at the angle where a branch originates. The bright-coloured eggs are very conspicuous on the brown bark. On the lower three feet of the trunk of a plum-tree badly attacked by aphis, I found within a week 42 patches of Coccinellid eggs—*A. bipunctata*, *H.* 14-*guttata*, *H.* 14-*punctata*, *C.* 11-*punctata*, and *C. variabilis*. Evidently there is a tendency to lay the eggs away from the light, but I have watched a *septempunctata* lay her eggs on a stone in bright sunlight. The usual period of incubation is three days, but it may extend to nine. The average laying period of the first two years' observations was 24 days. Incubation varied from 3 to 13 days, the average being 5 days in 1918, 4 in 1919, and 7¼ in 1920. Clausen (United States) finds the average incubation 5 days and the average egg-laying 28·2 days.

c. *The Larvæ.*

The larvæ when about to pupate are of a blackish-brown colour. The first upper lateral abdominal tubercle is always orange, and an orange patch extends across the abdomen between the fourth dorsal abdominal tubercles. This orange patch may be succeeded by similar patches of decreasing size and colour-intensity in the 5th, 6th, and 7th abdominal segments. In many cases there may be orange on the lower lateral tubercles of the fourth abdominal segment. The lower lateral tubercles may be surrounded by a cream-coloured ring (see note to Table I.). There is great variation in the depth of colour of the orange patches.

I have made many unsuccessful attempts to determine the differences in the larvæ and pupæ which are destined to become respectively Red and Black imagines. In 1918 the average larval period was 27 days, the minimum 22 and the maximum 27. In 1919 the average was 23, the minimum 16 and the maximum 39. Clausen found the average 16·1 days for the United States. In 1920 the average larval period was 35 days, the minimum 23, and the maximum 37.

d. *The Pupæ.*

The larvæ usually pupate on the under side of leaves, especially where the edge is curled up by aphis or drought. Pupæ are sometimes found on the upper side. In 1918 very few pupæ were found on the upper side of leaves, but in the early part of 1919, when there was a great deal of wet and cloudy weather, a much larger proportion was found on the more exposed surface. During the sunny part of July and August 1919 the pupæ were again rarely found on the upper side. I have found no special orientation of *bipunctata* pupæ, such as is so striking in *Anatis ocellata*, which both on the trunk and needles of the pine normally faces upwards.

The average length of pupation in 1919 was 13 days, the minimum 9 and the maximum 21. In 1919 the average was 17, the minimum 3 and the maximum 28. In 1920 the average was 20 days, the minimum 16, and the maximum 22. Clausen and Girault (**10** *a*) both found the American average 6 days. The very short period of three days was produced by placing the pupæ in a temperature of 101° F.

e. *The Imagines.*

On emergence the imagines vary from palest yellow to orange. Air and light usually produce the normal colour in a couple of days, but at times the original orange may persist for weeks. At certain seasons when *bipunctata* are emerging the majority caught are of an orange rather than the typical red colour. This observation applies also to *septempunctata* and *variabilis*. The variations of colour so obvious in some collections are not all true variations, but many are probably due to the development being still incomplete when the specimens were taken.

Although the Lady-bird which emerges in August or September may live to the following June, a period of ten months, its longevity during the summer is much shorter, the male sometimes dying after a mating-period of three weeks, although the female has lived two months after laying her eggs. Captivity would no doubt greatly modify this character.

The combined duration of incubation, larval life, and pupation varied from 28 to 56 days. The shortest period occurred during the very hot weather subsequent to July 22, 1919. Burgess (**1**) gives the complete period as 28 days in America, where the temperature would be very similar to that during this particular period in 1919.

Only a small percentage, 8 per cent. to 17 per cent., of the eggs laid became imagines. Palmer's results were better, as she obtained from 13 per cent. to 25 per cent. of imagines.

f. *The Enemies of the Lady-bird.*

The colour of the Coccinellids is supposed to be protective, and it is stated that they are not eaten by Insectivores. The yellow excretion produced by both larvæ and imagines is supposed to protect them from predaceous enemies. The latter contention appears to be partly based upon the fact that the excretion is disagreeable to Man both as regards taste and smell. Certainly the Lady-bird has some enemies besides parasitic flies. In this country the larvæ are eaten to some extent by Syrphid larvæ, for which reason it was imperative to examine carefully all leaves put in the breeding-boxes, as if any of these voracious Syrphids were inadvertently introduced, they soon made an end of the Coccinellid larvæ as well as the aphis. Spiders also eat these larvæ, as they have been found sucked dry in spider's webs on several occasions. In England I have observed Flycatchers and Sparrows taking *septempunctata* and *bipunctata*, and also found considerable numbers of the elytra of *septempunctata* in the droppings of Sea-Gulls when that Coccinellid was abundant on the coast. Elytra of *bipunctata* and *septempunctata* have been seen in the pellets of the Brown Owl. In America, Flycatchers and young Swallows are stated to eat Lady-birds. There also all stages of the Coccinellidæ are eaten by *Mantis religiosa* and a Wood-Bug, *Podisus serieventris* (**1**).

g. *Hibernation.*

The periodical appearance of vast numbers of various Coccinellids has long been known. These appearances are of two types: (1) increased numbers of the insects in various districts of the country during the spring or summer, in places where there were or had been large numbers of aphis; and (2) large numbers of the insects at specified places, usually in the spring or autumn, where there was or had been no food. In the latter case the insects are in close juxtaposition, and may occur in such quantities that the term "masses," used by Johnson, most fitly describes the case.

Septempunctata have occurred in masses by the seaside in England in the autumn, and Fabre (**10**) has observed them on Mount Ventoux in the Vaucluse Alps at a height of 4500 feet in June and October. This is a condition similar to *Hippodamia*, which is constantly found in large masses on the western American Mountains, where it is known that they gather to hibernate. The same phenomenon possibly also occurs in the Alps and other European mountains. The masses by the sea are probably pre- and post-hibernation gatherings. Johnson suggests that the yellow excretion may play some part in gathering these numbers together. If this is so at the time of hibernation, it may also be a factor in gathering Coccinellidæ together for feeding purposes.

In Staffordshire I have found hundreds of *septempunctata* swarming over sand-hillocks by the roads and on the commons, on warm days in April, at a time when they are beginning to emerge, in places where there is no sign of aphis. I have never found *bipunctata* in large quantities, although they do collect in small groups under bark for the winter hibernation. Mr. Alfred Priest reported to me the presence of large numbers of *bipunctata* in the neighbourhood of a disused chimney-stack in

September 1919. Early in 1920 he visited this place, and found large numbers of the insects lying massed upon one another in the cracks between the bricks where there was practically no shelter. The Lady-birds were on all sides of the chimney.

In September 1919 large numbers of *septempunctata* were reported from various parts of England, but in Staffordshire there were at the same time large numbers of *bipunctata* and *C.* 11-*punctata*, which, on account of their small size, were much less obvious. This abundance was entirely accounted for by the weather-conditions. Early in August there had been a period of warm fine weather during which aphis and Coccinellid larvæ flourished: this was succeeded by a wet, cold period, which no doubt retarded the pupæ; but when a second period of hot weather supervened, the retarded pupæ responded, as my breeding experiments show they will do, and simultaneously, instead of over a protracted period, the adults appeared.

4. *The Genetical Relations of the Varieties.*

Matings were made during the summers of 1918 and 1919. During the first year, only 22 of the 57 fertile matings produced a complete generation, the family in each case being reduced to one imago. In 1919, 23 complete generations were produced from 35 matings.

Eleven of these successful matings were Red × Red, and with the exception of one, Mating 32, produced only Red offspring, among which there occurred small variations from their parents and from "type." The Red bred true, producing none of the Black variety.

The exceptional mating (32) consisted of two Reds taken when mating. The female laid one small batch of eggs (7), from which two Black imagines were produced. Clearly the female was at the end of her productive period, and had probably mated with a Black before she was caught.

Six matings of Black × Black were made, five of which produced both Red and Black imagines, a phenomenon quite different from the Red × Red matings; but as it was not possible to guarantee that the females had not had partners previous to the scheduled one, it cannot at present be deduced that the genetic constitution of the Black as regards the purity of the genes is different from that of the Red.

The sixth mating (24), which produced only Blacks, was as follows:—♂ var. 4-maculata × ♀ 4-maculata produced five 4-maculata and one 6-pustulata. The female had certainly had no previous mate.

The five matings of Black × Black produced 8 Blacks and 4 Reds. It must be noted that these Reds were all variations from "Type" and not exactly like the Red parent. The problem therefore arises—are these variations heterozygous forms with an intermediate appearance? Similar varieties have, however, been found in the pure Red families, where, moreover, the variations of the offspring appear related to those of the parents; if, however, these variations are the heterozygous forms, one would expect to find some Blacks appearing when these Reds are mated together, but, so far, that has not been the case. A large number of matings will have to be made, as the numerical proportions in which the varieties occur in nature indicates that there are certain points of genetic stability, and that many of the intermediate varieties, if such there are, must have a definite relation to certain parent types.

The condition in *bipunctata* may be similar to that observed by Lutz (17) in *Crioceris asparagi*. He says: "Thus we have a good case of a perfectly graded variation (from spots discrete to spots joined) obeying Mendel's law. Spots joined even lightly and on one elytron only make a "pure" recessive individual. One of these intermediate forms seems characteristic of the (DR) heterozygous form."

Six matings as follows were made between Black and Red:—

m. 20 ♂ Red × ♀ 6-pustulata produced one Red.
m. 21 ♂ Red × ♀ 6-pustulata produced one 4-maculata, one 6-pustulata, two Red.
m. 22 ♂ Red × ♀ 4-maculata produced five 6-pustulata, three Red.
m. 23 ♂ Red × ♀ 6-pustulata produced four 4-maculata, five 6-pustulata, two Red.
m. 25 ♂ 4-maculata × ♀ Red produced one 4-maculata.
m. 29 ♂ Red × ♀ 6-pustulata produced one 4-maculata, two 6-pustulata, one Red.

There is here no sign of dominance, but there is a large proportion of Blacks (20) to the Reds (9). This proportion is surprising, as the Blacks are normally in the minority according to data so far collected. If the larvæ destined to become Black imagines have the same physiological response to heat as the Black imagines (see section 1), their large proportion might be accounted for.

So far, only two matings (m. 57 in 1918 and m. 25 in 1919) were made between a Black ♂ and a Red ♀; both these produced Black offspring only, so that not sufficient data is yet at hand to judge if there is a sex factor in the inheritance.

There are usually two medium posterior whitish spots on the pronotum of the Red form. These may be absent or the two may be large enough to fuse in the middle line. So far, no regular method of inheritance of these spots has been determined. Palmer (1911) found "the presence of the whitish basal markings on the pronotum (of *annectans* and *melanopleura*) dominate over its absence in *coloradensis* and *humeralis*." The degree of the development of these spots is not related to the degree of the development of the black dorsal spot in any way; these white spots are absent in the Black form, the pronotum of the Black and Red differing thus in degree of pigmentation. But those Red forms, in which the black spot even stretches as a band across the elytra, do not necessarily have a more pigmented pronotum than in "type." If an increase in the size of the black spot of "type" means a step forward in a melanistic direction, one would expect this tendency also to affect the pronotum.

C. variabilis.

C. variabilis has two forms of imagines, which in general colour arrangement are similar to the two principal forms of *A. bipunctata*. There is a Black form with ten red-ochreous spots and a Red (ochreous) form with fourteen black spots. The difference in the shade of the red between the two forms is much more marked than in *Adalia*. The red spots on the Black frequently tend to carmine at the edges, but the red ground-colour of the Red form would more accurately be described as ochreous; it is never as deep a red as occurs in *A. bipunctata* (type). I have no information of the percentages in which these types occur. The Black form of *variabilis* is the "type," but whether this indicates that it is the more common is unknown.

The dimorphism in *bipunctata* and *variabilis* is not equivalent to that of *Lina* (**18**), in which there is a spotted and a melanic form, for in that species there is certainly only one colour-pattern, as the spots can be sometimes seen in the melanic form by holding the wings up to the light. MacCracken (**18**) found the melanism recessive.

Two matings of *variabilis* were made: (1) mating 17, ♂ Black × ♀ Red produced 4 Red imagines; and (2) mating 18, ♂ Red × ♀ Black produced 4 Black and two Reds. As in *bipunctata*, there is no sign of dominance.

A third mating (10) was made between a ♂ Red *bipunctata* and a ♀ Black *variabilis*, the result of which was 7 Red *variabilis* and 5 Black *variabilis*. The two mated at intervals from May 29 to June 26, and during that period laid eggs as follows:—15 on June 3, 16 on June 4, 24 on June 12, 6 on June 18, and 15 on June 26; a total of 76. As the results were all *variabilis*, one cannot but suppose that the female was satisfactorily fertilised by a male of her own species before she was caught. This, however, involves the necessity that some of the spermatozoa remained capable of fertilization for 29 days at least; but Palmer states, p. 235 (**21**): "A female *Adalia* would not seem to be able to lay fertile eggs for more than three weeks after being isolated from a male."

On one point these two species differ considerably, for it is the Black form of *bipunctata* which is the more variable in the number of spots, whilst in *variabilis* it is the Red form which is the more variable. The recurrence of the same type of variation in species so nearly related and which constantly occur together, makes an understanding of the one imperative to a satisfactory understanding of the other.

5. *Summary.*

1. *Adalia bipunctata* has so many varieties that it is highly suitable for the needed study of inheritance of normally occurring variations.

2. *Adalia* can be mated in captivity with ease, but their cannibalistic habit makes it very difficult to rear them satisfactorily in large numbers.

3. The time passed in the various stages is variable, depending not only on the food, but also on the temperature, to which all stages, but especially the pupal, make a rapid response.

4. Little is known of either hibernation or migration, but apparently both *septempunctata* and *bipunctata* tend to collect in numbers in the spring and autumn, and may at times be found hibernating, piled upon one another, similar to the "masses" of *Hippodamia* found in the western U.S.A.

5. There is no evidence of dominance in crosses between the two main forms—the Red "type" and the Black (var. 4-maculata and var. 6-pustulata).

6. Eleven matings of Red × Red produced only the Red type.

7. Black and Red forms also occur in *C. variabilis*, and, as in *bipunctata*, neither is dominant.

8. The pronotum of the Black form is darker than that of the Red, but there is no progressive blackening of the pronotum of the Red coincidentally with the increase in the size of the black spots of the elytra.

9. Although it is possible to make a series from pure red elytra on the one hand through various patterns to pure black on the other, this cannot be regarded as proof that the variations are merely fluctuating. The percentages of the variations is, as far as is known, approximately stable, and certain types are far more common than others. These facts, combined with the observation that the children tend to show the variations of the parents, strongly suggest that there are probably certain points of genetic stability, and that only analysis is needed to show that there is some regular method of inheritance.

I have much pleasure in thanking Dr. A. D. Imms for naming several of the aphis species and Mr. W. B. Grove for naming the mould, *Cladosporium aphidis*, which he believes has never before been recorded as British.

LITERATURE.

1. Burgess, A. F. 1903.—Economic Notes on the Family Coccinellidæ. U.S. Dept. Agric. Div. Ent., Bull. 40 (New Series), pp. 25–32.
2. Burgess, A. F., & Collins, C. W. 1911.—The Value of Predaceous Beetles in destroying Insect Pests. U.S. Dept. Agric. Year-Book, pp. 453–466.

3. Clausen, C. D. 1915.—A Comparative Study of a Series of Aphis-Feeding Coccinellidæ. Journ. Econ. Ent. vol. viii. pp. 487–491.

4. Chyzer, Bela. 1886.—Note on Cannibalism of Coccinellidæ. Revatani Lapok. vol. iii. p. 107.

5. Curtis, John. 1860.—Farm Insects. London: pp. 71–73.

6. Donisthorpe, H. 1919.—Myrmecophilous Lady-bird, *Coccinella distincta* Fald.: its life-history and association with Ants. The Entom. Record, 1919, vol. xxxi. No. 12, pp. 214–222, & 1920, vol. xxxii. No. 1, pp. 1–3.

7. Dunning. 1869.—Discussion on swarms of Coccinellæ, Nov. 1869 by Mr. Dunning. Trans. Ent. Soc. London, p. xxv.

8. Ewing, H. E. 1914.—Some Coccinellid Statistics. Journ. Econ. Ent. vol. vii. pp. 440–443.

9. Ewing, H. E. 1913.—Notes on Oregon Coccinellidæ. Journ. Econ. Ent. vol. vi. pp. 404-407.

10. Fabre, Henri. 1897.—'Souvenirs Entomologiques.' The chapter entitled "Les Emigrantes."

10 *a*. Girault, A. A. 1914.—Pupal Stages of *Adalia bipunctata*. Ent. News, vol. xxv. p. 155.

11. Holtz, Martin. 1907.—Ueber *Adalia bipunctata* L. typ. und deren Varietat sex-pustulata L. Ent. Woch., 24 Jahrg. pp. 181–182.

12. Johnson, Roswell. 1907.—Economic Notes on Aphids and Coccinellids. Ent. News, vol. xviii. pp. 171–174.

13. Johnson, Roswell. 1910.—Determinate Evolution in the Colour-pattern of Lady-beetles. Carnegie Inst., No. 122

14. Johnson, Roswell. 1912.—Heredity of Colour-Pattern in Coccinnellid Beetles (abstract). Proc. 7th Int. Zool. Congress. Cambridge, Mass., pp. 409–410.

15. Krause. A. H. 1904.—*Adalia bipunctata* Varietaten aus Nord-Thüringen. Ent. Zeits. vol. xviii. p. 112.

16. Lutz, K. G. 1888.—Hibernation of the Two-spotted Lady-bird. (Correspondence.) Insect Life, vol. i. p. 56.

17. Lutz, F. E. 1908.—Notes on the Inheritance of Variations in the Colour-pattern of *Crioceris asparagi*. 'Psyche,' Boston, vol. xv. pp. 50–52.

18. McCracken, I. 1906.—Inheritance of Dichromatism in *Lina* and *Gastroidea*. Journ. Exp. Zool. vol. iii. pp. 331-336.

19. Meissner, Otto. 1912.—Statistik und Biologie von *Adalia bipunctata*. Ent. Zeits. vol. xxvi. pp. 82–83, 87–88, 94–95.

20. Meissner, Otto. 1912.—Cannibalismus bei Coccinelliden. Wien. Ent. Zeit. vol. xxvi. p. 322.

21. Palmer, Miriam A. 1911.—Some Notes on Heredity in the Coccinellid genus *Adalia* (Mulsant). Ann. Ent. Soc. America, vol. iv. pp. 283–302, 4 pls.

21 *a*. Palmer, Miriam A. 1914.—Some Notes on the Life-history of Lady-beetles. Ann. Ent. Soc. America, vol. vii. pp. 213–237, 2 pls.

22. Reichart, A. 1904.—*Adalia bipunctata* (L.) varietaten. Ent. Jahrb. Leipzig, vol. xiii. pp. 179–181, 1 Taf.

23. Schröder, Chr. 1901 & 1902.—Die Variabilitat der *Adalia bipunctata*, gleichzeitig ein Beitrag zur Descendez-Theorie. Allg. Zeits. für Ent., Bd. vi. (1901), Nos. 23 & 24, pp. 355, 371; Bd. vii. (1902), pp. 5, 37, 65, mit Tafel 5 und 5 Textabbildungen.

24. Schröder, Chr. 1904.—Selektions und der Theorie der Zeichungs-phylogenie bei den Lepidoptera. Allg. Zeits. für Ent., Bd. ix. pp. 215, 249, 281.

25. Schröder, Chr. 1909.—Die Erscheinungen der Zeichnungsvererbung bei *A. bipunctata* und ihren ab. 6-pustulata u. 4-maculata. Zeits. wiss. Inseckten biol. Berlin, vol. iv. pp. 132–134.

26. Slater, J. W. 1889.—Cannibalism with Lady-birds. Insect Life, vol. ii. p. 55.

27. Smith, J. B. 1892—General Notes: *Epilachna borealis*. Insect Life, vol. v. Nov., p. 98.

28. Smith, J. B. 1893.—Carnivorous and Herbivorous Insects. Ent. News, vol. iv. p. 123, figs. 1 & 2.

Birmingham, November, 1920.

31. Filariid Worms from Mammals and Birds in the Society's Gardens, 1914–1915. By C. L. Boulenger, M.A., D.Sc., F.Z.S., Professor of Zoology, University of the Panjab, Lahore.

[Received September 1, 1920: Read November 16, 1920.]

(Text-figures 1–12.)

INDEX.

	Page
Introduction	491
Filaria subcutanea v. Linst.	492
Acanthocheilonema diacantha (Molin)	494
,, *gracile* (Rud.)	496
Dicheilonema horridum (Dies.)	499
Diplotriæna tricuspis (Fedtsch.)	499
,, *diucæ*, sp. n.	501
,, *flabellata* (v. Linst.)	502
Filaria aramidis, sp. n.	503

In February 1914, I was asked by the Prosectorial Committee to undertake the identification of the Nematode parasites obtained at the Society's Gardens, and material was forwarded to me from the Prosectorium at regular intervals until the beginning of 1916. During this period monthly reports, containing provisional identifications, were sent to the Committee, the material being laid aside for further investigation. My study of the collection thus accumulated was interrupted by my departure for Mesopotamia on war service, and was only resumed three years later at the end of 1919.

The material described in the present memoir consists of the representatives of the Family Filariidæ obtained from Mammals and Birds in the Gardens. Altogether eight species were met with, two of which are described as new. Of the known forms, three have been previously observed on single occasions only and are species about which further information was desired; the other three are worms commonly reported from Zoological Gardens; yet even of these our knowledge is by no means complete, and I have therefore added a short account of two of them to my descriptions of the less known species.

During recent years renewed attempts have been made by various authors, especially Railliet and Henry, to break up the old genus *Filaria* s. l., and have resulted in a much improved knowledge of many of the commoner Filariids; some of the older generic names proposed by Viborg, Diesing, etc., have been revived and several new genera established. In this paper, I have attempted, wherever possible, to refer the worms described to these new groupings.

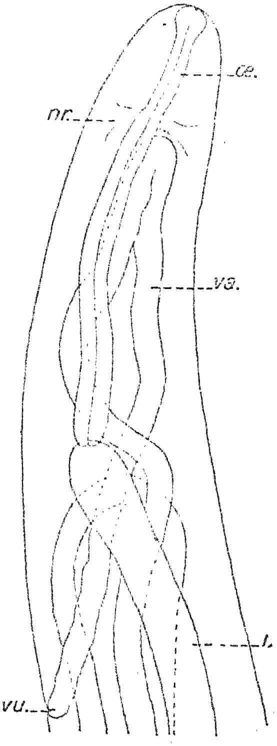
Genus FILARIA Mueller, 1787.

FILARIA SUBCUTANEA v. Linstow, 1899, non Parona, 1894.

A number of specimens of this species were obtained from the subcutaneous tissue of the Canadian Porcupine, *Erethizon dorsatum*.

This species, which is known only from the type-specimens obtained from the same host in the Berlin Zoological Gardens, is of special interest, for, as pointed out by Hall (1916), there is reason to believe that *F. subcutanea* v. Linst. is a synonym of *F. martis* Gmelin, the species generally regarded as the type-species of the genus *Filaria* s. str.

Text-figure 1.



Filaria subcutanea v. Linst.

Lateral view of the anterior extremity of female. × 38.

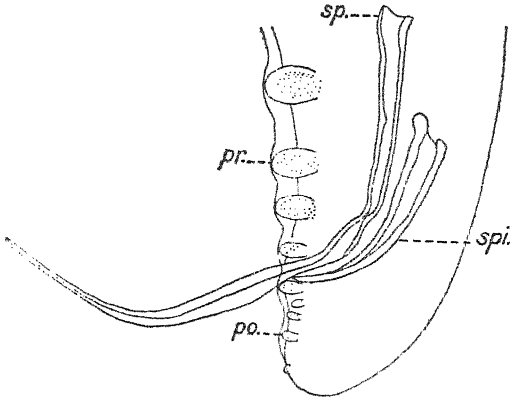
i., intestine; *n.r.*, nerve-ring; *œ.*, œsophagus; *va.*, vagina; *vu.*, vulva.

My account of *F. subcutanea* will be found to differ in some respects from that given by v. Linstow, yet I think there is little doubt that we have both dealt with the same form. *F. martis* is very imperfectly known, and until new material is described the relationship between the two species must remain doubtful; there are certain characters, *e.g.*, the position of the vulva, which in our present state of knowledge it is impossible to reconcile.

Hall has pointed out that v. Linstow's specific name is a homonym of *F. subcutanea* Parona, 1894. I have followed his example and refrained from renaming the species until its proper relationship with *Filaria martis* is ascertained.

My material was obtained from the same animal as the microfilaria recorded by Plimmer (1915) in his annual report on the blood-parasites; Hall is therefore right in assuming that this larval stage is to be referred to *F. subcutanea* v. Linst.

Text-figure 2.



Filaria subcutanea v. Linst.

Posterior extremity of male, lateral view. × 225.

po., postanal papilla; *pr.*, preanal papilla; *sp.*, short spicule; *spi.*, long spicule.

Specific diagnosis.—Filaria: Body filiform, more attenuated posteriorly than anteriorly, both extremities rounded.

Cuticle appears smooth except under very high magnifications, when a fine transverse striation is apparent.

Head-papillæ very small, four submedian papillæ present, lateral papillæ not noted.

Œsophagus simple, *i.e.* not divided into anterior and posterior regions, and short.

Male 48–56 mm. long, with a maximum thickness of about 0·45 mm. Œsophagus 1·2–1·4 mm. in length.

The posterior end of the body is coiled in a loose spiral and provided with cuticular alæ at its extremity. Cloaca 0·07 mm. from the posterior extremity. There seem to be nine pairs of papillæ, of which four are preanal and five postanal. The papillæ of the last pair are small and flat; they no doubt correspond to the similar pair at the posterior extremity of the female. The eight anterior pairs of papillæ are elongated and decrease in size from before backwards.

The two spicules are very unequal, measuring 0·38–0·42 mm. and 0·13–0·14 mm. respectively. The long spicule consists of an anterior tubular region followed by a partly membranous posterior region. The small spicule is conical and terminates in a point.

Female 160–175 mm. in length, with a maximum thickness of about 0·7 mm. The œsophagus measures 1·5–1·7 mm. in length. Anus about 0·15 mm. from the posterior extremity, the latter rounded and provided with a pair of small flat papillæ. At the level of the anus the body has a thickness of 0·2 mm.

Vulva 1·9–2·4 mm. from the anterior extremity. The slender vagina has a forwardly directed loop which extends to the level of the nerve-ring, 0·4 mm. from the oral end.

Ovoviviparous. Eggs thin-shelled, measuring 0·022 mm. × 0·015 mm.

Genus ACANTHOCHEILONEMA Cobbold, 1870.

ACANTHOCHEILONEMA DIACANTHA (Molin, 1858).

Filaria diacantha was originally described from worms obtained in the abdominal cavity and lungs of various Rodents in Brazil. The specimens from the Society's Gardens are from the Canadian Porcupine, *Erethizon dorsatum*, and were found in the peritoneal cavities.

The original description is somewhat incomplete, and Hall, in his monograph of the Nematode parasites of Rodents (1916), is inclined to regard this form as a species of *Setaria*; the well preserved material before me makes it, however, quite clear that the worm is to be referred to Cobbold's genus *Acanthocheilonema* as recently redefined by Railliet, Henry, and Langeron (1912).

Specific diagnosis.—*Acanthocheilonema*: Body slender, filiform, diminishing in breadth at both extremities and much attenuated posteriorly. Anterior extremity somewhat claviform, the head being separated from the rest of the body by a slight, neck-like constriction.

The cuticle appears longitudinally lined under a low power of the microscope; high magnifications, however, reveal a very fine transverse striation.

Six head-papillæ are present, four submedian and two lateral. The lateral papillæ are large and project in such a way that the head appears almost square in dorsal or ventral view.

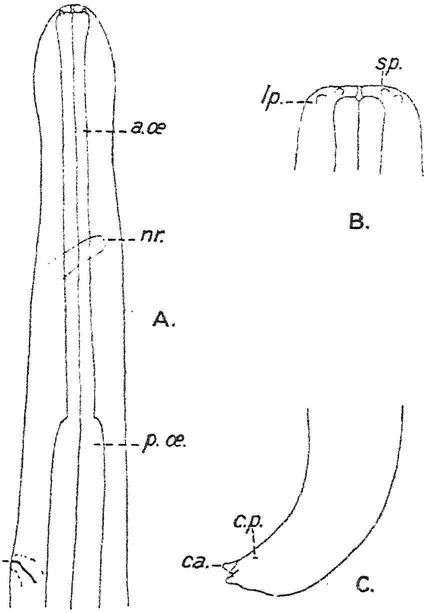
The œsophagus consists of distinct anterior and posterior regions; the former is narrow and measures under 0·5 mm., the posterior region is stouter and has a length of 2·3 mm. The nerve-ring surrounds the middle of the anterior part of the œsophagus.

The caudal region is long and slender, and its extremity in both sexes is provided with a pair of conical appendages; in front of these on the ventral surface is a pair of small flat papillæ.

Male 35–40 mm. long, its greatest breadth about 0·25 mm. The head has a breadth of only 0·07 mm.

The posterior end of the body is coiled in a loose spiral. Cloacal aperture 0·25–0·28 mm. from the extremity. Male papillæ small, consisting of five pairs, four preanal and one post-anal close behind the cloaca.

Text-figure 3.



Acanthocheilonema diacantha (Molin).

A. Lateral view of anterior extremity of female. × 120. B. Dorsal view of head. × 225. C. Tail of female, lateral view. × 225.

a.œ., anterior region of œsophagus; *c.a.*, caudal appendage; *c.p.*, caudal papilla; *l.p.*, lateral head-papilla; *n.r.*, nerve-ring; *p.œ.*, posterior region of œsophagus *s.p.*, submedian head-papilla; *v.*, vulva.

The unequal spicules measure 0·14 and 0·11 mm. in length respectively; the longer spicule is tubular in shape, with a somewhat ill-defined membranous posterior region, the smaller spicule is in the form of a strong tube, bent in the middle.

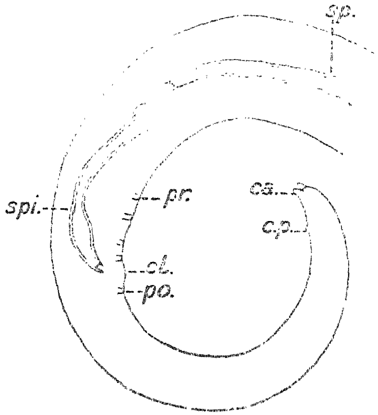
Female 58–65 mm. in length, with a maximum breadth of about 0·35 mm. Head 0·08 mm broad.

Anus about 0·2 mm. from the posterior extremity.

Vulva 0·65–0·9 mm. from the anterior end. The long vagina runs almost straight backwards.

Ovoviviparous. Eggs thin-shelled, measuring 0·03 × 0·02 mm.

Text-figure 4.



Acanthocheilonema diacantha (Molin).

Posterior extremity of male, lateral view. × 225.

c.a., caudal appendage; *cl.*, cloaca; *c.p.*, caudal papilla; *po.*, post-anal papilla; *pr.*, preanal papilla; *sp.*, long spicule; *spi.*, short spicule.

ACANTHOCHEILONEMA GRACILE (Rudolphi, 1819).

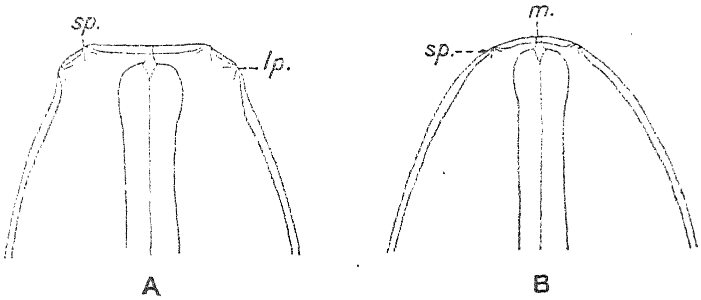
Filaria gracilis is a common parasite of Monkeys and has been listed from more than twenty-five species, including both Old-World and New-World forms. My material is derived from the peritoneal cavities of the following species, all from the Society's Gardens: White-fronted Capuchin (*Cebus hypoleucus*), Smoky Woolly Monkey (*Lagothrix infumata*), Moustache Marmoset (*Leontocebus mystax*), and Squirrel Monkey (*Saimiris sciurea*).

The systematic position of this worm is somewhat uncertain. Diesing, in his famous 'Revision der Nematoden' (1860), placed it in his genus *Dipetalonema*, a genus which is not only ill-defined, but contains also widely separate forms from Birds and Reptiles. In many of its characters, *e.g.*, position in the host, structure of head-papillæ, œsophagus, caudal appendages, spicules, etc., *Filaria gracilis* closely resembles certain species of *Acanthocheilonema*, and I have decided to include it, at least provisionally, in this genus.

Specific diagnosis.—Acanthocheilonema: Body filiform, very elongated, much diminished in breadth posteriorly. Head narrow, not separated from the body by a neck-like constriction.

Cuticle with very fine transverse striations, only visible under high magnifications.

Text-figure 5.

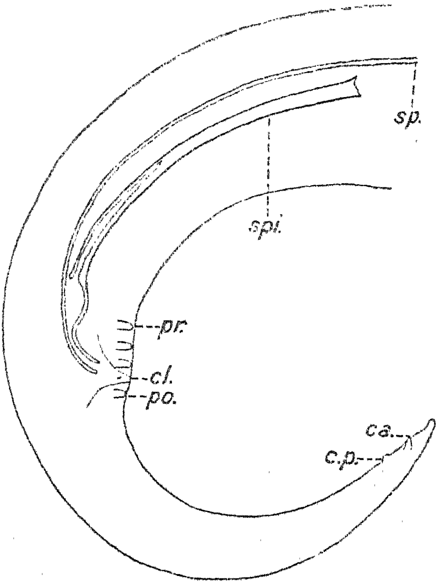


Acanthocheilonema gracile (Rud.).

Head: A. Dorsal view, B. Lateral view. × 225.

l.p., lateral head-papilla; *m.*, mouth; *s.p.*, submedian head-papilla.

Text-figure 6.



Acanthocheilonema gracile (Rud.).

Posterior extremity of male, lateral view. × 225.

c.a., caudal appendage; *c.p.*, caudal papilla; *cl.*, cloaca; *po.*, postanal papilla; *pr.*, preanal papilla; *sp.*, posterior part of long spicule; *spi.*, short spicule.

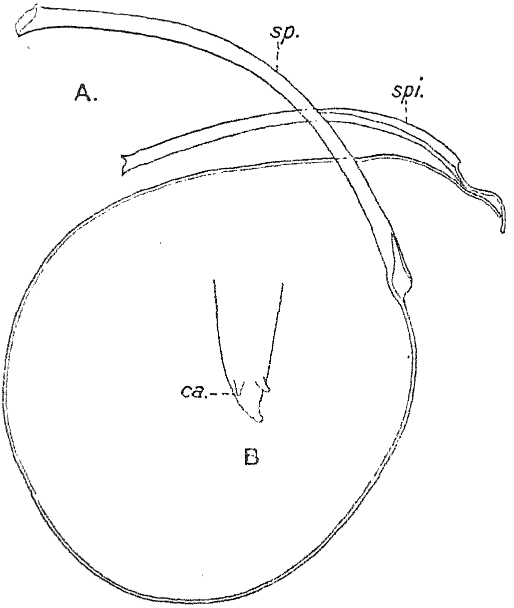
Six head-papillæ, the lateral pair prominent giving the head a truncated appearance when viewed from the dorsal or ventral surface.

Œsophagus consisting of unequal anterior and posterior regions.

Caudal region long and very slender, in both sexes provided with a pair of conical appendages.

Male 96–110 mm. in length, with a maximum thickness of about 0·27 mm. Head 0·09 mm broad.

Text-figure 7.



Acanthocheilonema gracile (Rud.).

A. Spicules of male. × 225. B. Caudal extremity of female. × 225.
ca., caudal appendage; *sp.*, long spicule; *spi.*, short spicule.

The posterior end of the body is very slender and coiled in a loose spiral. Cloaca 0·26–0·28 mm. from the extremity. Three or four pairs of preanal papillæ and one pair of postanal papillæ close to the cloaca. A pair of small conical appendages are situated 0·02 mm. from the posterior extremity; just anterior to them are a pair of small flat papillæ.

Spicules very unequal; the long spicule is 1·23 mm. long, and consists of an anterior tubular region, 0·33–0·36 mm. in length, followed by a long thin terminal region; the short spicule measures 0·27 mm., it also has the shape of a tube, terminating in a membranous, hooked extremity.

Female 160–250 mm. long, with a greatest thickness of about 0·38 mm. Head 0·11 mm. broad.

The anterior region of the œsophagus measures 0·58 mm., the posterior 2·5 mm. in length.

Caudal region with a pair of elongated appendages, about 0·03 mm. from the end of the body. Anus 0·63 mm. from the extremity.

Vulva 0·8-1·15 mm. from the oral end. The long, straight vagina is directed posteriorly and has a length of 8 mm.

Ovoviviparous. Eggs small and thin-shelled, measuring 0·015–0·018 × 0·01 mm.

Genus DICHEILONEMA Diesing, 1860.

DICHEILONEMA HORRIDUM (Diesing, 1851).

Examples of this well-known species were sent to me from the Prosectorium on two occasions; they were obtained from the body-cavity of *Rhea americana*. It is a worm commonly reported from Zoological Gardens.

Genus DIPLOTRIÆNA Railliet et Henry, 1909.

The genus *Diplotriæna* was established by Henry (in Henry and Ozoux, 1909) to include a group of very closely allied species of *Filaria* from the body-cavities of various birds, chiefly Passeriformes. They are easily recognised by the presence of a peculiar apparatus in the form of a pair of chitinous "tridents" situated in the front of the head, and by the structure of the male spicules, one of which is straight, the other twisted.

Fifteen species have been referred to this genus; the majority have, however, been so imperfectly described that their recognition is very difficult. The material from the Society's Gardens includes three species which are to be placed in this genus; two of these I have referred to established species, the third is described as new. Diagnoses of the species of *Diplotriæna* must be regarded as merely provisional until a thorough revision of all known forms has been made.

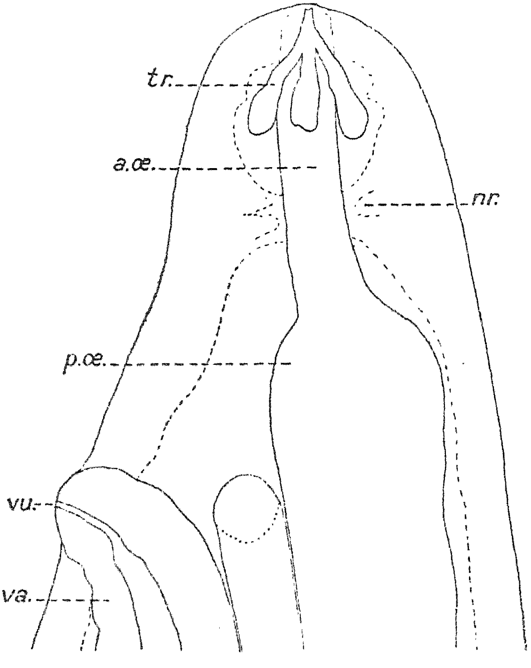
DIPLOTRIÆNA TRICUSPIS (Fedtsch., 1883).

Stossich's monograph of Filariids (1897) shows that *Filaria tricuspis* has been recorded from a large number of different Birds; the measurements given in his specific diagnosis make it clear, however, that a number of species have been confused under this name.

The specimens which I have referred to *D. tricuspis* were found in the body-cavities of the White Headed Starling, *Poliopsar leucocephalus*; in their measurements they agree fairly well with the worms described by v. Linstow (1891) as belonging to this species. My material consisted of females only.

Specific diagnosis.—Diplotriæna: Body long, filiform, tapering close to the anterior and posterior extremities which are of approximately the same thickness. Cuticle not transversely ringed.

Text-figure 8.



Diplotriæna tricuspis (Fedtsch.).

Lateral view of anterior extremity of female. × 120.

a.œ., anterior region of œsophagus; *nr.*, nerve-ring; *p.œ.*, posterior region of œsophagus; *tr.*, trident; *va.*, vagina; *vu.*, vulva.

Six head-papillæ; the four submedian are very small and inconspicuous. The œsophageal trident has a length of 0·15 mm.; its anterior stem is truncated.

Œsophagus consisting of a short anterior region and a very long posterior region. The nerve-ring surrounds the anterior œsophagus about 0·25 mm. from the anterior extremity.

Female 160–180 mm. long; the greatest breadth of the body is about 0·6 mm.

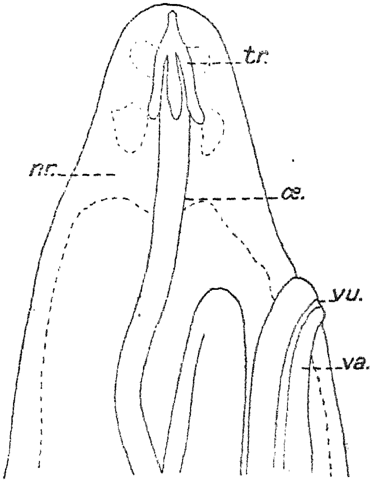
The narrow anterior region of the œsophagus has a length of

0·35 mm., the wider posterior region 8·8 mm. The anus is subterminal.

Vulva 0·55–0·6 mm. from the oral extremity. The stout, muscular vagina runs straight backwards, and has a length of 25 mm.

Oviparous. Eggs thick-shelled, 0·045–0·05 × 0·035 mm., containing well-developed embryos.

Text-figure 9.



Diplotriæna diucæ, sp. n.
Lateral view of anterior extremity of female. × 120.
Lettering as in the preceding text-figure.

DIPLOTRIÆNA DIUCÆ, sp. n.

This worm was obtained from the body-cavity of the Diuca Finch, *Diuca grisea*; the material included both male and female specimens.

Specific diagnosis.—Diplotriæna: Body comparatively short, semi-transparent, tapering at both ends. The anterior extremity is narrower than the posterior.

Cuticle thin, transversely ringed.

Cephalic extremity with six very inconspicuous, flattened papillæ.

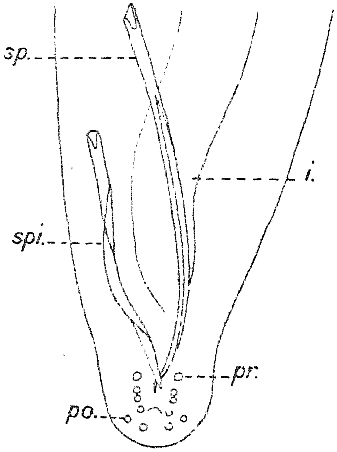
Each œsophageal trident has a length of 0·13–0·14 mm.; its anterior stem terminates in a fine point. Œsophagus 2·5–4 mm. long, narrow throughout, and without division into anterior and posterior regions. The nerve-ring surrounds the œsophagus 0·2 mm. from the anterior extremity.

Male 12–20·5 mm. long, with a maximum breadth of about 0·75 mm.

Cloaca 0·06–0·07 mm. from the posterior extremity. Tail broad and rounded. There are six pairs of inconspicuous, flattened papillæ; four pairs are preanal, two postanal.

Spicules unequal; the long spicule is straight and has a length of 0·72 mm., the short spicule is twisted and measures 0·45 mm.

Text-figure 10.



Diplotriæna diucæ, sp. n.

Posterior extremity of male, ventral view. × 75.

i., intestine; *po.*, postanal papilla; *pr.*, preanal papilla; *sp.*, long spicule; *spi.*, short spicule.

Female 30–43 mm. in length; the body attains a thickness of 0·9 mm.

Anus about 0·1 mm. from the rounded extremity. The vulva projects slightly from the ventral surface, 0·35 mm. from the cephalic end. Vagina short, 0·9–1 mm. in length.

Oviparous. Eggs thick-shelled, measuring 0·045–0·05 × 0·03 mm.

DIPLOTRIÆNA FLABELLATA (v. Linstow, 1888).

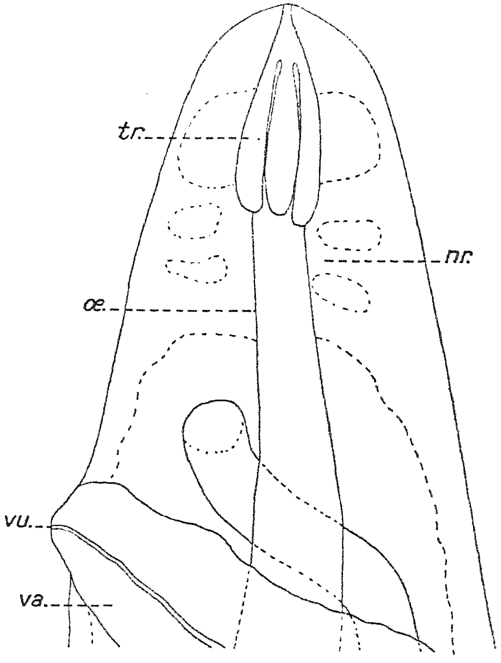
My material includes a single specimen of a female *Diplotriæna* from the body-cavity of the Red Bird of Paradise, *Paradisea rubra*. I take it to be the same species as *D. flabellata* described from *Paradisea apoda* by v. Linstow in the 'Challenger' Reports (1888).

Specific diagnosis.—*Diplotriæna*: Body short, more attenuated anteriorly than posteriorly.

Cuticle transversely ringed. Œsophagus not divided into two regions, narrow anteriorly, increasing in width gradually behind the nerve-ring, the latter 0·3 mm. from the oral end.

Trident 0·25 mm. long, its anterior stem truncated.

Text-figure 11.



Diplotriæna flabellata (v. Linst.).

Lateral view of anterior extremity of female. × 120.

Lettering as in the preceding text-figures.

Female 44 mm. in length, with a maximum thickness of about 1 mm. Caudal extremity rounded, broader than the head. Position of anus not ascertained.

Vulva prominent, 0·6 mm. from the anterior extremity; the thick muscular vagina has a length of 2 mm.

Oviparous. Eggs thick-shelled, 0·04–0·045 mm. × 0·25 mm.

INCERTÆ SEDIS.

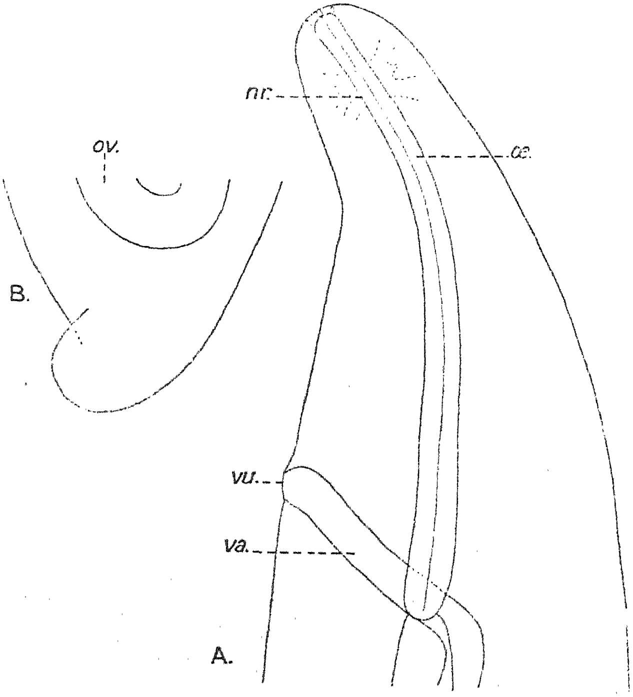
FILARIA ARAMIDIS, sp. n.

A single specimen of this species was obtained from the leg-muscles of the Cayenne Rail, *Aramides cayennensis*. In the absence of the male it is impossible to place the form in its proper systematic position; I have, therefore, retained it in the genus *Filaria* s.l. In some respects it appears allied to certain species known from the muscular system of Mammals, *e.g.* *Filaria scapiceps* Leidy (Hall, 1916).

Specific diagnosis.—*Filaria* s.l.: Body comparatively short and thick, tapering nearly equally at both extremities.

Cuticle finely striated transversely.

Text-figure 12.



Filaria aramidis, sp. n.

A. Anterior extremity; B. Posterior extremity. Lateral view. × 75.
Lettering as in the preceding text-figures. *ov.*, loop of ovary.

Head rounded, bearing four very small submedian papillæ; lateral papillæ not seen.

Œsophagus narrow and simple, *i.e.*, not divided into anterior and posterior regions. Nerve-ring close to the anterior extremity.

Female 25 mm. in length, with a maximum breadth of about 1 mm. Width of head 0·2 mm. The œsophagus has a length of 1·1 mm. Posterior extremity rounded; position of anus uncertain, about 0·15 mm. from the end of the body.

Vulva 0·82 mm. from the anterior extremity; the slender vagina is directed posteriorly and has a length of 2·4 mm.

Eggs thin-shelled, measuring 0·03–0·035 × 0·02 mm.

Bibliography.

Diesing, K. M. (1861).—"Revision der Nematoden." Sitzungsber. d. Kais. Akad. Wiss. Wien, xlii. 1860, pp. 595–736.

Hall, M. C. (1916).—"Nematode Parasites of Mammals of the Orders Rodentia, Lagomorpha, and Hyracoidea." Proc. U.S. Nat. Mus. Washington, l. pp. 1–258.

Henry et Ozoux (1909).—"La Filaire du Foudi." Bull. Soc. Path. Exot. Paris, ii. pp. 544–547.

Linstow, O. von (1888).—"Report on the Entozoa collected by H.M.S. 'Challenger' during the years 1873–6." 'Challenger' Reports, xxiii. pp. 1–18.

—— (1891).—"Ueber *Filaria tricuspis* und die Blutfilarien der Krähen." Arch. f. Naturg. Berlin, lvii. p. 292.

—— (1899).—"Nematoden aus der Berliner Zoologischen Sammlung." Mitt. a.d. Zool. Samml. d. Mus. f. Naturk. Berlin, i. (2). pp. 1–28.

Plimmer, H. G. (1915).—"Report on the deaths which occurred in the Zoological Gardens during 1914, together with a list of the blood-parasites found during the year." Proc. Zool. Soc. London (1), pp. 123–130.

Railliet, A., Henry, A., et Langeron, M. (1912).—"Le genre *Acanthocheilonema* Cobbold, et les Filaires péritonéales des Carnivores." Bull. Soc. Path. Exot. Paris, v. pp. 392–395.

Stossich, M. (1897).—"Filarie e Spiroptere. Lavoro Monografico." Bull. Soc. adriat. di sci. nat. Trieste, xviii. pp. 11–162

32. The Fauna of the African Lakes: a Study in Comparative Limnology with special reference to Tanganyika. By William A. Cunnington, M.A., Ph.D., F.Z.S.

[Received May 31, 1920: Read November 16, 1920.]

(Text-figures 1–2.)

Index.

	Page
Historical Survey	567
General Introduction	512
Systematic Account and Lists of Species	518
General Discussion and Conclusions	592
Summary	609
Bibliography	613

1. HISTORICAL SURVEY.

Ever since the days of the great African explorers and their quest of the sources of the Nile, there has existed a certain fascination about the big lakes of Central Africa. While the scientific world was at first concerned principally with the geography of the heart of the continent, opportunity soon offered of learning something of the organisms which live in the vast inland seas, and it then became evident that matters of no little biological interest were involved.

It is the object of this paper to deal in comparative fashion with the animals of the principal lakes, and since Tanganyika* holds a unique position as regards its fauna, a somewhat detailed account of its zoological exploration seems fitting, as it will afford both an introduction to a study of the lakes and an enumeration of certain outstanding facts.

Little more than sixty years have passed away since Burton and Speke, the first Europeans to penetrate to Lake Tanganyika, reached the shores of this big inland sea. Their expedition, after encountering numberless hardships, arrived at the lake between the Malagarasi River and Ujiji on the thirteenth of February, 1858. Although little was done in the way of exploring Tanganyika, Burton described, with a surprising degree of accuracy, various facts concerning it which he learned from the Arabs and natives, while Speke, on his return, brought certain shells from the lake shore, which came into the possession of the British Museum.

---

* Some years ago I called attention to the orthography of the name 'Tanganyika,' advocating the adoption of the spelling 'Tanganika' by English writers (69). The arguments advanced in favour of the change have not lost their force, and still seem worthy of consideration. As there is no indication that writers in this country are prepared to accept the modification, I adhere reluctantly to the old form.

It was in the examination of these shells that the unusual interest which still attaches to certain forms of life found in Tanganyika had its origin. S. P. Woodward, who reported on the collection, was struck by the fact that some of the shells were curiously marine in appearance. Of one of them, which he named *Lithoglyphus zonatus* (now known as *Spekia zonata*), he said (**205**, p. 348) that it so much resembled a *Nerita* or *Calyptræa* that it might have been taken for a sea-shell. Of another, he remarks that "Its colour, solidity, and tuberculated ribs give it much the appearance of a small marine whelk (*Nassa*)." At the time, these opinions attracted little attention, although the matter was destined to come into prominence at a later date.

Some twenty years later—in 1878—there was established the first settlement of Europeans on the shores of Tanganyika, when agents of the London Missionary Society settled at Ujiji in August of that year. With praiseworthy public spirit, the Directors of the Society had given instructions that the gathering of scientific information should be considered among the duties of this pioneer expedition, and thus it is that E. C. Hore (**101**), a member of the party, was the first to attempt a systematic collection of the forms of life occurring in the lake. While the collections since made by trained naturalists have, of course, added very largely to the knowledge of the fauna and flora, the forms obtained by Hore embraced many different groups, and afforded the first comprehensive glimpse of the organisms which the lake contains.

This English Mission was very shortly followed by the establishment of a French Catholic Mission, and it should be noted that these White Fathers of Algeria have also been instrumental in gathering information, and in particular have made large collections of shells which have been described in later years by French conchologists.

At the end of 1879, Tanganyika was visited by Joseph Thomson. Collections of shells made by Hore and Thomson were reported on by Edgar Smith in 1880 and 1881 (**159, 160, 161**), and he also had occasion to remark on the marine appearance of some of them. This matter being brought to the front once more, Thomson put forward the view (**190**, vol. ii. p. 85) that the water of the lake had probably been saline until recent geological times, when it became freshened through circulation and outflow to the Congo (compare also **191**, where he goes further, and suggests the origin of the lake from a former sea occupying the Congo basin).

The discovery of medusæ by Böhm (**114**), a German explorer who crossed Tanganyika in 1883, only emphasised matters and laid stress on the supposed marine character of the lake fauna, since, with few exceptions, such organisms are confined to the ocean. Von Wissman (**204**, p. 253) confirmed this discovery when sailing on the lake in 1887, and a few years later, F. L. M. Moir, the manager of a British trading company, undertook to obtain specimens of these medusæ properly prepared for scientific investigation. This valuable material, on its arrival in England at the end of 1892, was placed for examination in the hands of R. T. Günther of Oxford.

It was Günther who first put forward a detailed theory to account for the presence in a central African lake of animals with apparently marine affinities. In his report on the Tanganyika medusa he suggested (**95**, p. 289) that if at some early period the interior of Africa stood at a much lower level, with the Atlantic Ocean extending over the Congo basin and the lake existing as an arm of the sea, it would then be possible readily to explain the presence in it both of the medusa and the remarkable molluscan forms. As the lake became separated from the sea, so the salinity of the water would tend to decrease if it were supplied with inflowing rivers and found an outlet through which to carry away the salt.

Since the problem presented by Tanganyika had now become so interesting and definite, it seemed very desirable that the lake fauna should be investigated upon the spot by some trained zoologist. The matter was taken up by Ray Lankester, who, with the help of others interested in the question, obtained the necessary grants from the Royal Society and organised the First Tanganyika Expedition. This was put in charge of J. E. S. Moore of the Royal College of Science, who from that time onwards contributed largely to the knowledge of the lakes of Central Africa.

The expedition left England in the autumn of 1895, and Lake Shirwa was visited as well as Nyasa, while Moore spent several months on the shores of Tanganyika. As a result of this journey, the original problem seemed far from being solved, for the expedition brought matters to light which only made the lake appear more remarkable. Many strange and unique animal forms were collected, certain of which were thought to show marine affinities, while the majority were new to science. The collection included a number of types not unexpected in a tropical lake; only a proportion of the fauna exhibiting the unusual features to which reference has been made. Moreover, although the expedition had visited Nyasa and Shirwa, in neither of these lakes had marine-like forms been found resembling those of Tanganyika.

Through a study of the newly acquired material, especially the anatomy of certain of the molluscs, Moore arrived at the conclusion that the forms exhibiting a marine appearance could not be compared directly with any marine types of the present day, but rather possessed archaic and generalised characters which suggested that they were the relics of a marine fauna of a previous age. Further, he considered that some of the Tanganyika shells offered a strong resemblance to certain marine Jurassic fossils, in particular those of the Inferior Oolite of the Anglo-Norman basin. Taking this as evidence of the period from which these remarkable living forms had been derived, Moore propounded once more a theory of the former connection of Lake Tanganyika with the sea, asserting that this connection existed in Jurassic times (**131**).

The discoveries of the First Tanganyika Expedition, while stimulating interest in the faunas of the African lakes, only emphasised the need for further information. It was still to be determined whether any of the other big lakes contained organisms with a marine appearance, and it was very desirable that more should be learned of the geology of the Tanganyika basin, as having a direct bearing on the question of a former connection with the sea. Ray Lankester, therefore, took the initiative once more, formed a committee of scientific men interested in the subject, and organised a second expedition. In view of the geological and geographical work to be undertaken, a liberal grant was made by the Royal Geographical Society, and Moore was accompanied by Malcolm Fergusson as surveyor and geologist. The Second Tanganyika Expedition (**136**) left England in 1899, and after proceeding up lakes Nyasa and Tanganyika, visited Kivu, Edward Nyanza*, and Albert Nyanza before returning to the coast by way of the Victoria Nyanza.

An examination of the collections obtained in the latter lakes only laid additional stress on the unique nature of Tanganyika, for in none were found animals suggestive of the sea. Indeed, the already long list of forms found only in Tanganyika was augmented by the expedition, more particularly as regards the fish. Certain of the little-known regions between Tanganyika and the Albert Nyanza were mapped, and considerable attention was paid to the study of the geology of this district as well as that of the Tanganyika basin. Not long after the return of the expedition, Moore published a volume entitled "The Tanganyika Problem" (**137**), in which he dealt at some length with the question which had so occupied his attention. A large amount of new information was given in this work. It treated in a comprehensive manner the physiography and geology of the part of Africa concerned, and besides giving a complete review of the fauna of Tanganyika as then known, discussed the origin of fresh-water faunas in relation to the matter.

While a great deal of information bearing on the geology and geography of the lake regions had been obtained, and extensive collections had afforded a knowledge of the fauna of Tanganyika, the flora of the lake had not been dealt with as it deserved. To those who had been impressed with the marine characteristics of certain animals living in the lake, it appeared quite conceivable that when the flora came to be investigated, plants equally remarkable and equally suggestive of marine affinities would be discovered. If, for example, specimens of the red Algæ so characteristic of the ocean were to be found, this would afford very valuable evidence concerning the ancient history of the lake.

---

* The lake, formerly known as the Albert Edward Nyanza, is always referred to in this paper as Edward Nyanza or Lake Edward. The change of name was approved by the late King Edward, and should be universally adopted in order to avoid confusion with the Albert Nyanza or Lake Albert (*cf.* **55**, p. 129).

It was with this end in view that a Third Tanganyika Expedition (68) was organised by the Committee, with the conduct of which I had the honour of being entrusted. One of the principal objects of this expedition was therefore to make a careful collection of the water plants of Tanganyika, at the same time collecting in Nyasa, with the idea of affording a comparison with a more normal African fresh-water lake. My instructions also provided "That other groups of organisms likely to throw light on the Tanganyika Problem, and especially fishes, shall not be neglected." Including observations on various points of interest, the work before the expedition was thus sufficiently extensive, although matters of geology and geography were outside the field of enquiry.

I left England in the spring of 1904, proceeding via the Zambezi and Shiré rivers to Lake Nyasa, where a few weeks were spent in collecting. My stay on and around Tanganyika lasted about eight months, which were fully occupied in making collections and observations as far as facilities offered. Returning to the coast by way of the Victoria Nyanza, an opportunity was afforded of obtaining representatives of the flora of that lake for purposes of comparison with the plants collected in Nyasa and Tanganyika.

It may at once be stated that the flora of Tanganyika fails to exhibit quite the remarkable features which some had expected it to show. As regards the higher aquatic plants, a comparison of the species from Tanganyika with those from Nyasa and Victoria Nyanza does not throw any light on the hypothesis of a marine origin for Tanganyika. The fresh-water Algæ of the lake, however, have proved to be a strange and interesting assembly, a considerable number being peculiar to Tanganyika while several show undoubted marine affinities. The lower forms of vegetable life which occur thus tend to confirm the unique biological nature of the lake.

On the zoological side, my collections have added not a little to the number of forms known from the lakes, the results appearing as a series of memoirs principally in the Proceedings of the Zoological Society. For the first time systematic townettings were made in Tanganyika on an extensive scale, and as a result, detailed information is to hand about whole groups of organisms, only the bare existence of which in the lake was known before. Thus reports have now been published on the smaller Crustacea (Copepoda and Ostracoda) as well as on the Rotifera, while in addition the groups Branchiura and Hydrachnida are new records from the lake.

In completing this brief review of the zoological exploration of Tanganyika, it is only necessary to refer to the Belgian expedition to that lake and to Lake Mwero undertaken by the late Louis Stappers. This expedition visited Tanganyika in 1912–

1913, and brought back valuable information concerning the depth of the lake and the salinity of its water, as well as representatives of its fauna. A large collection of fishes was found to contain a number of new species, brief diagnoses of which have been published (**32, 33, 37**), but beyond this, so far as I am aware, no further particulars have been forthcoming, owing to the outbreak of the European war and the subsequent lamented death of Stappers.

2. GENERAL INTRODUCTION.

This paper aims, in particular, at giving an account of the animal forms now known to occur in Lake Tanganyika, but while special attention has been directed to enumerating these, types from other lakes have been noticed and discussed. The account is therefore a comparative survey, and shows clearly the remarkable nature of the fauna of Tanganyika to which reference has frequently been made.

It must, of course, be understood that the systematic review and the deductions drawn therefrom, are of necessity based upon present knowledge, and may need modification in the light of future discoveries.

In order not to exceed reasonable limits, the scope of the paper has been restricted, and it does not deal with all the big lakes of Africa. At the same time, the largest and most important lakes have been considered, and only those of lesser interest are outside the field of enquiry. Whenever a tabular form has been adopted, columns for the lakes are uniformly arranged in the following order:—Tanganyika, Victoria Nyanza, Nyasa, Albert Nyanza, Edward Nyanza, and Kivu.

It is not possible to consider here at any length the geography and physical features of the lakes concerned, but certain outstanding particulars may be mentioned.

With the exception of Victoria Nyanza, all the lakes under review occupy portions of the Great Rift Valley, as it has been called, and are, therefore, of a very characteristic type. Without entering into details, it may be briefly explained that Suess, in discussing the geology of Central Africa, put forward the view that the long deep valleys which run through the country in an approximately north and south direction have been caused by trough-faulting on an extended scale. Each "Graben"—as he terms these long narrow valleys, with their steep, almost precipitous sides—he believes to have been produced by the faulting and sinking of a long narrow tract of country, and it is but natural that a number of these characteristic depressions are filled with water. Thus Tanganyika and the other typical "Graben" lakes are situated in long trough-like valleys, bounded for the most part by steeply rising sides, which may reach in places a height of two or three thousand feet above the level of the water.

From the very nature of the troughs in which the lakes are situated, the latter are likely to be deep, with shores quickly shelving, and this is precisely what investigation reveals. Both Nyasa and Tanganyika have now been pretty adequately sounded, and the figures obtained are very remarkable for fresh-water basins. Nyasa shows a maximum depth of about 786 metres (430 fathoms), while Tanganyika reaches no less than 1435 metres (about 784 fathoms)[*]. Tanganyika is thus the second deepest lake in the world, Lake Baikal coming first, while Nyasa takes fourth place, following the Caspian Sea. Where sufficient soundings have been taken, the contours constructed show in a number of instances the remarkably steep shores which were only to be expected in such cases.

Victoria Nyanza, as already indicated, is a lake of a very different nature from those of the Great Rift Valley. With a length of some 200 miles and a breadth of 130 miles, it has roughly the form of a parallelogram. While it has the largest area of any of the African lakes, it occupies only a shallow depression, and instead of being bounded by steeply rising shores two or three thousand feet in height, the surrounding hills reach a maximum of 300 feet or so. The greatest depth is a mere 73 metres (40 fathoms).

In most other respects, the lakes included in this survey do not differ greatly so far as physical conditions are concerned. They are all large sheets of water, where consequently almost oceanic conditions prevail, while the three biggest lakes are subject to storms of a violent description. In dealing with the evidence afforded by the plants and animals inhabiting them, this fact must not be overlooked, as physical surroundings may have induced some of the features which are noted.

Although extending considerable distances both north and south of the equator, these lakes all exist under practically the same climatic conditions. They are tropical lakes, and differences in fauna and flora are clearly not to be correlated with the very slight climatic variations which may possibly occur.

The temperature of the water is naturally high. I took sufficient temperature readings during my visit to Tanganyika to afford some idea of the general conditions, although an exhaustive survey was impossible. Only a few figures need be mentioned here. The lowest reading I ever obtained in Tanganyika was 73·3° Fahr. and the highest 81·0°. Surface readings at different periods of the year varied only between 74·7° and 81·0°, and an average of 51 observations gave a mean of 78·0°. At considerable depths the water temperature remains relatively constant, for readings taken at a depth of about 139 metres (76 fathoms)—the length of the sounding line—on various occasions and at different places only vary between 74·8° and 74·1°. Stappers gives the temperature of the surface water as oscillating between 25° and 28° C. (77°–82·4° F.) (**176**). Marquardsen, however, quotes exactly 25·0° C. (77° F.) as a mean of 70 surface readings made by Jacobs. The latter was also able to carry out deep water observations, to which Marquardsen refers as follows:—"Unter 400 m. bis in die grössten Tiefen liegt dann eine fast homotherme Wasserschicht von 23·15° bis 23·12°" (73·67°–73·61° F.) (**111**, p. 97). A less extended series of water temperature observations was made in Nyasa * and also in Victoria Nyanza during the Third Tanganyika Expedition, but the figures are sufficient to show that there are no important differences from the results obtained in Tanganyika. It is obvious that the amount of water lost by evaporation must be very great in all these cases.

---

[*] For further details concerning Nyasa, consult Moore (**134**, p. 7) and Rhoades (**148**)—concerning Tanganyika, see Stappers (**174** & **175**) and Marquardsen (**111**).

As far as I am aware, there is relatively little known concerning the nature of the water in these African lakes. They are considered in general terms to be "fresh" †, but, except in certain instances, no analyses have been made, and the nature and quantity of the salts dissolved in the water are unknown. The information which is to hand regarding Tanganyika and Kivu makes it clear that they differ from normal fresh waters, and this difference appears to be reflected (as will be shown in due course) in the nature of the organisms they contain. Tanganyika water, while containing a relatively small amount of calcium salts, is unusually rich in salts of magnesium (**176**). Lake Kivu is an extreme case, where the salinity is very high. In this instance, salts of calcium appear to have been almost entirely replaced by considerable amounts of sodium and magnesium salts, the latter being quite excessive in quantity (**103**).

It is possible that the water of Tanganyika has somewhat changed in nature within recent years, for most of the early explorers agree that the water was brackish, or at least "peculiar" in taste. If the rather vague statements are to be relied upon, this alteration in salinity is probably to be associated with the question of the outflow of the lake. A period during which the lake possessed no outlet would result in an accumulation of salts producing brackish water, while a subsequent period with a regular outflow would diminish the quantity of saline matter in solution. An examination of the available records suggests that something of this kind has taken place, and it thus becomes necessary to consider the whole subject of the outflow of Tanganyika.

This is not the place to discuss in detail all the evidence which bears on the matter, but the conclusions arrived at may be summarised as follows:—Since the area drained is not very great, and the rainfall is relatively low, the amount of water which finds its way into the lake is nearly balanced by the evaporation (*cf.* **190**, vol. ii. p. 68 *et seq.*). It follows that under average conditions there will be little change in the surface-level and no occasion for an outlet for the surplus water. There are reasons for believing that at some former period the waters of Tanganyika did not flow out at all, and were consequently more saline than at present. As a result of the formation of great volcanic cones north of Lake Kivu, that portion of the Nile drainage system which once drained north into Edward Nyanza became cut off, and its waters finally diverted southwards into Tanganyika (*cf.* **137**, p. 89 *et seq.*).

---

* Certain observations concerning Nyasa were made by Fülleborn (**83**, p. 334 *et seq.*).

† Grogan, referring to Lake Edward, says:—"Although the water was salt, it was drinkable" (**91**, p. 191). In the same connection Bright remarks:—"The water of Albert is drinkable, but not good" (**55**, p. 138).

Slowly raised in level by this additional supply, the water eventually found an outlet to the west, along the course of the Lukuga, a former affluent, and through a sandstone ridge denuded in part by the action of a tributary of the Congo. The lake having risen abnormally before the establishment of an outlet, sank at first rapidly, remaining at a lower level, subject to fluctuations with the time of year and the amount of rainfall. A few consecutive seasons of unusual drought would suffice to reduce the level of the lake to a point at which all outflow would cease. It seems likely that under such circumstances a barrier might be formed in the bed of the effluent, due to the combined effects of wind-blown sand and tropical swamp vegetation, and varying in nature with the length of time taken to produce it. If a tolerably firm dam was formed, a considerable rise in the level of the lake would be necessary in order to develop enough power to sweep away the obstruction. There is reason to believe that the high water level which Cameron and Stanley observed, and the subsequent re-establishment of an outflow, were phases in a cycle of this nature. If a periodicity of this kind really exists, it must of necessity be extremely variable in nature, and due to irregularities in the rainfall.

The important bearing of these inferences on the problem of the fauna of Tanganyika it is hardly necessary to emphasise. If the Nile has lost a not inconsiderable drainage area, which has been added to that of Tanganyika, it seems very reasonable to suppose that this accession of water produced, for the first time, the overflow of the lake. If this supposition be correct, Tanganyika must have been completely isolated and without an outlet, until the formation of the great volcanic dam in geologically recent times.

The lists of animals from the various lakes given in the body of this work are, as regards extent, partly dependent on the amount of biological exploration which each lake has received. That is to say, a comparatively small fauna may be merely due to less complete examination. Whether the lakes considered here can be regarded as having been at all equally investigated, it is not easy to pronounce, but I incline to the view that at the present time the disproportion—if any—is not great[*]. It is perhaps the smaller lakes which have been less fully explored, and from them, therefore, new records might be expected, although their smaller size does not offer the same occasion for other organisms to come to light. The larger lakes, more thoroughly, but still incompletely explored, may well from their very vastness contain a number of forms which have never yet been observed or collected. On the whole then, while recognising that future investigations will probably add considerably to the records from the individual lakes, there is reason to believe that a comparative survey of the forms at present known will afford a relatively true conception of the actual state of affairs.

It is not so easy as might at first sight appear, to give complete and satisfactory lists of the animals known to inhabit the lakes in question. I do not refer only to the difficulties of synonymy, though these are by no means inconsiderable, particularly where the Mollusca are concerned. There is also the difficulty of deciding which forms should be regarded as true aquatics, since there are of necessity a number of types which are on the border line. While in some groups the question does not arise, in others it is clearly impossible to draw a hard and fast distinction between aquatic and non-aquatic species. Thus in making a decision in individual cases, as was necessary for the purposes of this paper, I may have excluded forms which some think should have been included and *vice versâ*. For example, I have deliberately excluded all reference to the Aves, although the lakes are well stocked with water-fowl, and similarly I omit the group Insecta, notwithstanding the presence of water beetles and insect larvæ. Certain Oniscidæ were in the collections which I brought from Nyasa and Tanganyika, the specimens having been obtained from the lake shore. These truly terrestrial Isopods are likewise omitted from the systematic portion of the paper, as are also certain of the Oligochæte worms. All these types, while moisture-loving, are obviously not to be associated with individual lakes, and their precise distribution cannot have the significance which attaches to the distribution of strictly aquatic species.

There is finally the problem of deciding whether forms recorded from the neighbourhood, but not actually from the waters of a particular lake, are to be reckoned as belonging to that lake's fauna or not. This becomes, in a sense, a matter of special importance when a species is described as endemic[†]. Should a species, for instance, be regarded as peculiar to a certain lake when it was actually obtained from a neighbouring swamp? I have dealt with the difficulty in what seems the most commonsense way, by definitely including all forms recorded from the drainage area of a lake as belonging to it. Nevertheless it must be pointed out that even this decision does not avoid the trouble altogether, for it is not an easy matter to determine what constitutes the drainage area of a lake in a country where the boundaries of river basins are quite indefinite in the rainy season. Again, the possibility is not excluded, that organisms from adjoining fresh-waters may not find physical conditions suitable for them in the big lake in their vicinity, in which case they should not be included in its fauna. Evidence of the existence of this very phenomenon is to be found as regards certain plankton organisms which are absent from both Tanganyika and Kivu. Throughout this paper I have placed a § against the names of all species which have not definitely been recorded from the waters of the lake in question.

---

[*] As concerns Nyasa, the collections of Fülleborn do not come only from the lake itself, but also from adjacent ponds, swamps, and rivers. Regarded in this light, Nyasa has been more thoroughly investigated than the other lakes, where records from the surrounding neighbourhood are almost unknown.

[†] It is necessary to explain that I use this word deliberately in the sense of peculiar to a locality, *i. e.* not found elsewhere. While the word is often used with this significance in works on geographical distribution, its meaning is a little ambiguous, and it is desirable to make the matter quite clear.

Subject to these difficulties in compiling exact lists, the following approximate figures can be given:—Tanganyika contains 402 species of which no less than 293 are endemic, Nyasa with a total of 361 and 86 endemics coming second. Victoria Nyanza has a somewhat smaller total, viz. 289, but a larger number of endemic forms (110). The three smaller lakes show a great falling off in numbers, Albert Nyanza mustering only 67 species of which 9 are endemic and Edward Nyanza 54 with 11 endemic species. Kivu, finally, only contains 23 types in all, 4 of which are peculiar to the lake. Thus, as regards its fauna, Tanganyika is distinguished from the other lakes not only by containing a larger number of forms, but especially by displaying a remarkable proportion of endemic species.

While it is not necessary to discuss here the origin of fresh-water organisms, a few observations on one aspect of the question are needed at this stage. By movements of the earth's crust, portions of the sea have, from time to time, been cut off with their inhabitants, and by gradual freshening have been subsequently converted into fresh-water lakes. During the latter process, there is little doubt that certain of the organisms would be unable to withstand the change and would perish. Inland lakes which appear to be the modified remainders of isolated portions of the ocean are sometimes spoken of as "relict lakes" (Reliktenseen). It is, of course, precisely this view of the origin of Tanganyika which was put forward by Günther and afterwards elaborated by Moore. On this hypothesis, the peculiar fauna was originally that of a former sea, then that of a salt lake, and finally that of a fresh-water lake.

The marine-like appearance of certain of the Gasteropod shells of Tanganyika was expressed by the conchologist Bourguignat by employing the term "thalassoid" with reference to them—a term which did not commit its author to any view as to origin (**42**, p. 9). In his paper "On the Zoological Evidence for the connection of Lake Tanganyika with the Sea," Moore indicated his belief in the origin of these forms as relicts from a former ocean, by introducing the expression "halolimnic" (**126**, p. 453: compare also **138***). Of course from Moore's point of view, a number of animals from other groups—all those, in fact, which he believed to be the remains of an old marine fauna—are similarly to be included under the term halolimnic. It is necessary for an understanding of what follows, that the significance of these words should be explained at this point.

It remains to give a systematic account of what is known of the animal groups represented in the lakes, after which an attempt will be made to draw conclusions from the facts which this detailed study reveals.

I wish to take this opportunity of acknowledging my indebtedness to the experts who have so willingly examined and reported on the collections I made in Africa. In a number of cases, too, they have given me valuable advice during the compiling of those sections of this paper on which they are authorities, and for this also I express my thanks.

3. SYSTEMATIC ACCOUNT AND LISTS OF SPECIES.

In dealing in systematic fashion with the groups of animals which are reviewed in detail, the latter are arranged approximately in order, beginning with higher and ending with lower types. No attempt is made to conform to any particular scheme of classification, the headings employed being merely such as are sufficient to indicate the contents of the different sections. Where certain animal groups are conspicuously wanting, it should be understood that they are either intentionally omitted, as not truly aquatic forms (*cf.* p. 516), or are unrepresented in the lakes. In each case a list is given (in tabular form where more than a few types are concerned) of the species hitherto recorded from the different lakes, and this is followed by a brief discussion of the points of interest and of the significance of the records. The complete discussion of the zoological evidence and the conclusions to which it points is deferred until the general survey which follows the systematic account.

MAMMALIA.

The biggest, though by no means the most interesting inhabitant of the lakes of Central Africa, is the hippopotamus, which is widely distributed in the tropical parts of the continent. The common species, *Hippopotamus amphibius*, is probably to be found in all the lakes under review *, but definite records are not in every case available.

---

* I do not agree with Moore's subsequent statement that types which are thalassoid cannot be halolimnic. It is true that the words are not synonymous, but surely organisms may be marine-like in appearance (thalassoid) and at the same time relict types (halolimnic).

In addition to the hippopotamus, there are two species of otter which occur over the greater part of Africa, and there is little doubt that both of these frequent the waters of the big lakes. A specimen of the larger form—now known as *Aonyx capensis*—from Lake Victoria is in the collection of the British Museum. The smaller otter is known as *Lutra maculicollis*. Hore refers to the occurrence of otters in Tanganyika (**101**, p. 150), and both Grogan and Bockelmann speak of them in Kivu (**91**, p. 123: **16**, p. 371), but actual records are wanting in most cases. It may nevertheless be safely assumed that both species form a part of the fauna of the lakes with which this paper is concerned.

As far as I am aware, these are the only Mammals † which are recorded from the lakes.

CROCODILIA.

The largest reptile and the one most in evidence in the African lakes, is, of course, the crocodile, which is extremely widely distributed in tropical Africa. Two species ‡ have been recorded as occurring in Lake Tanganyika.

1. *Crocodilus niloticus.*

This is the common African crocodile with the most extended distribution, ranging from Palestine to Natal and known also from Madagascar. It is found in Nyasa and Victoria Nyanza as well as in Tanganyika (see British Museum Catalogue (**19**) and lists given by Tornier (**192, 193**, and **194**)), but, as far as I can ascertain, it has not been definitely recorded from the other big lakes, though it very probably occurs in them all ‖.

2. *Crocodilus cataphractus.*

Recorded from Ujiji, eastern shore of Tanganyika, by Tornier (**194**, p. 579). Essentially a West and Central African form, extending from the Senegal to the Gaboon and nearly all over the Congo.

OPHIDIA.

Four snakes adapted to an essentially aquatic life have been found on the shores of Lake Tanganyika. In addition to these, a snake allied to the cobras was taken swimming in the lake during the Third Tanganyika Expedition. The five species* may be enumerated as follows:

---

* Grogan states that the hippopotamus is not found in Kivu (**91**, p. 122), and Bockelmann and Hundeshagen refer to this also (**16**, p. 371: **103**, p. 204).

† Carl Peters, in his book "New Light on Dark Africa," English translation, London 1891, speaks on page 445 of having seen porpoises in the Victoria Nyanza. There is to my mind little doubt that he was misled, either by the appearance of an otter or even perhaps by one of the great fishes of the lake.

‡ For specific distinctions and synonymy consult Boulenger (**19**, p. 278 *et seq.*).

‖ A statement is made by Schubotz (**156**, p. xix) that there are no crocodiles in Lake Edward, but this does not agree with the accounts given by other travellers. Grogan (**91**, p. 122), Bockelmann (**16**, p. 371), and Hundeshagen (**103**, p. 204), however, speak of the absence of crocodiles from Kivu.

1. *Tropidonotus olivaceus.*

This is a well-known and common water-snake which is distributed over nearly the whole of Tropical Africa. It has also been recorded from Victoria Nyanza (**180**, p. 265) and Edward Nyanza (**192**, p. 67), and may very well occur in most of the other big lakes.

2. *Glypholycus bicolor.*

Brought from Tanganyika by Hore, one of the earliest collectors, and also recently obtained from the same locality. In contrast to the preceding, this form has been found nowhere else. The genus was established by Günther (**93**, p. 629) to receive this species, but a second species has since been found in Nyasaland†.

3. *Grayia ornata.*

A Tropical African snake, distributed in the west from the Cameroons to Angola and extending eastwards to the Uellé and Ituri. Recently recorded from Albertville on the western shore of Tanganyika.

4. *Grayia tholloni.*

Known from the Congo region, the Upper Nile, and the western shore of the lake.

5. *Boulengerina stormsi.*

This snake, which belongs to the same group as the cobras, is probably highly poisonous, but not strictly aquatic in character. The species was described from a single specimen (a young one, 24 cm. long) discovered by Storms on the western shore of Tanganyika. A second specimen, which was obtained by my expedition, was taken actually swimming in the lake. It is in all probability adult and measures 125 cm. This form has not been obtained elsewhere.

From an examination of this list it will be seen that more is known of the snakes of Tanganyika than of those of the other big African lakes, from which indeed there are but two definite records—to wit, those of *Tropidonotus olivaceus* in Victoria

---

* For particulars relating to these snakes, as also synonymy and means of identification, consult Boulenger (**34**: **35**).

† The Nyasaland species of *Glypholycus*—*G. whytii*—is also a truly aquatic snake, and may quite well occur in Nyasa, although it has not hitherto been reported from that lake.

Nyanza and Edward Nyanza. Although Tanganyika has certainly received a considerable amount of attention, this circumstance would not alone suffice to explain the relative richness of its Ophidian fauna, which is the more remarkable in that two of the species are endemic forms. It is hardly among the snakes that types characteristic of a lake would be expected, but they nevertheless afford an interesting parallel to the state of affairs which is so constant and striking in most of the groups of typically aquatic animals.

CHELONIA.

Five species of aquatic tortoises come within the scope of this survey*, of which four have been found in Tanganyika.

1. *Sternothærus sinuatus.*

A form well known from Tanganyika and obtained by Stuhlmann in the Victoria Nyanza (**192**, p. 4). It has more recently been reported from Nyasa (**193**, p. 583) and from Lake Albert (**180**, p. 200), while it is widely distributed in South Africa and in East Africa south of the equator.

2. *Sternothærus derbianus.*

This species appears to be more especially West African, but also occurs in Tanganyika.

3. *Sternothærus nigricans.*

A specimen of this tortoise from Usumbura, Lake Tanganyika, is referred to by Sternfeld in his report on the reptiles of the German Central Africa Expedition (**180**, p. 201). It is also known from the region of Mozambique and from Madagascar.

4. *Pelomedusa galeata.*

This is likewise a widely distributed form, and is recorded by Tornier (**193**, p. 583) both from Tanganyika and Victoria Nyanza. It has again been reported from Victoria Nyanza by Sternfeld (**180**, p. 201), and the British Museum also possesses a specimen from that locality. The species does not seem to have been mentioned hitherto from any of the other big lakes, although it is well known from Southern and Tropical Africa and occurs even as far north as the Sinaitic Peninsula.

5. *Cycloderma frenatum.*

This well-known Zambezi type has been collected by Fülleborn

---

* Particulars of these Chelonians will be found in the British Museum Catalogue (**19**).

(**193**, p. 583 & **194**, p. 580) in Lake Nyasa also. It is not known from any other African lakes.

In this case again a larger number of forms is on record from Tanganyika than from the other Central African lakes, but the species are all widely distributed, and their precise distribution in the lakes is probably a matter of little significance. A curious piece of negative evidence of considerably more interest is the fact that, with one exception, there are no records of Trionychidæ from any of the lakes, although these forms are so eminently aquatic and are known from other localities in Central Africa. The exception to which I refer is Tornier's allusion (**193** & **194**) to *Cycloderma frenatum*, a Zambezi species, in Lake Nyasa.

BATRACHIA.

While there are many Batrachians which are widely distributed in the African continent, the number of truly aquatic forms—with which alone this paper is concerned—is very small. So far as I am aware, the only true aquatics found in the lakes of Africa belong to the Anuran genus *Xenopus*, of which two species* need to be enumerated.

1. *Xenopus muelleri.*

This form appears to be rather the commoner of the two. The British Museum collection contains specimens from Lakes Tanganyika and Nyasa, and according to Tornier (**192**, p. 162) this species was collected by Stuhlmann at Bukoba on Victoria Nyanza. Its occurrence does not seem to have been recorded from any of the other big lakes, but as it is widely distributed in the Eastern parts of Tropical Africa, it is quite likely that it may exist in them too.

2. *Xenopus lævis.*

Recorded by Tornier (**192**, p. 163) from Victoria Nyanza. Subsequently recorded by Nieden (**141**, p. 186) from the same lake and also from the western bank of the Rusisi River which flows into Tanganyika—though not reported actually from the latter lake itself. This form likewise has an extended distribution in Central Africa, and may very well occur in the other lakes also.

Since both these species are so widely distributed, it is probable that their exact distribution in the lakes is of little moment.

---

* For the distinctions between the two species of *Xenopus* consult Boulenger (**27**, p. 249).

PISCES.

The fish of Tanganyika constitute no inconsiderable proportion of the animal forms which are known from the lake, since there are now recorded from its waters no less than 146 species. This result is mainly due to the activities of the three British expeditions and more recently the Belgian expedition under the late Louis Stappers, though a number of smaller collections have added considerably to our knowledge.

There was a period during which the fish fauna of Tanganyika had probably been more carefully investigated than those of the other big lakes, but at the present time this is no longer the case. So far as Victoria Nyanza is concerned, this is due particularly to the researches of the late W. G. Doggett, M. Alluaud. E. Degen, and E. Bayon, while in Lake Nyasa the recent collectors have been F. Fülleborn and E. L. Rhoades. It is nevertheless very doubtful whether all the fish forms which inhabit these vast inland seas have as yet been even approximately discovered, for each extensive collection still adds new species, often of very striking appearance. At the same time it will be agreed that the investigations of many explorers, spread over a fairly considerable period of years, must have furnished data on which it is possible to rely, even though further knowledge may occasion some revision in points of detail.

The fishes are better represented in the lakes than any other group. Nyasa appears to form an exception, as in that case the number of Rotifera even exceeds that of the fishes. This is due to the inclusion of a large number of extra-lacustrine records.

In the list which follows, 308 species of fish are enumerated, and it is a point of considerable interest that only three of these are recorded from outside the continent. They are *Clarias lazera*, *Tilapia nilotica*, and *Haplochromis desfontainesii*, all known from Syria, with which, through the valleys of the Jordan and Nile, there is believed to have been communication in former geological times.

The outstanding features in the case of Tanganyika will be seen to be firstly the large number of different forms found within the limits of a single lake, and secondly the remarkably large percentage of those forms which are not known to occur elsewhere.

Table of Distribution of Pisces †.

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Kivu.	Other parts of the world.
Family Polypteridæ.							
Polypterus congicus	P*	...	...	...	...	...	Congo R.
„ senegalus	...	...	...	P	...	...	W. Africa, Nile.
Family Lepidosirenidæ.							
Protopterus æthiopicus	P	P	...	...	P	...	Nile, Soudan.
Family Mormyridæ.							
Mormyrops deliciosus	...	...	P	...	...	...	W. Africa, Zambezi.
Petrocephalus catostoma	...	...	P	...	...	...	Rovuma R.
„ degeni		E					
Marcusenius nigricans	...	P	...	...	...	..	East Africa.
„ discorhynchus ..	P	...	P	...	...	..	Zambezi.
„ petherici	...	P §	...	...	...	...	Nile.
Gnathonemus longibarbis ...	...	E	...	...	...	...	Victoria Nile.
Mormyrus kannume	...	P	...	...	...	..	Nile.
„ longirostris	P	...	P	...	...	...	Bangweolo, Zambezi.
Family Clupeidæ.							
Pellonula miodon	E						
Stolothrissa tanganicæ........	Gen. E						
Family Characinidæ.							
Hydrocyon forskalii	...	...	...	P	...	...	W. Africa, Nile.
„ lineatus	P	...	...	...	...	...	Tropical Africa.
Alestes dentex	...	...	...	P	...	...	W. Africa, Nile.
„ macrophthalmus	P	...	...	P? ‖	...	...	Mweru, Congo, Gaboon.
„ sadleri	...	E	...	...	...	...	Malawa R.
„ nurse	...	P	...	...	...	...	W. Africa, Nile.
„ jacksonii	...	E §	...	...	...	...	Malawa R.
„ imberi	..	...	P	...	...	..	Congo, Zambezi.
„ vittatus.................	E						
„ rhodopleura	E						
Citharinus gibbosus	P	...	...	...	...	..	Congo R.

† For further details relating to the Pisces, see in particular the comprehensive 'Catalogue of the Fresh-water Fishes of Africa,' by G. A. Boulenger (**36**), which is the authority on which, in the main, I have relied in preparing the adjoining list. It is necessary to make it quite clear that I follow Boulenger in regarding (1) the fishes obtained from that part of the Victoria Nile which lies between Lake Victoria and the Murchison Falls as belonging essentially to the lacustrine and not to the Nile fauna, and (2) the fish collected from the Upper Shiré River (as opposed to the Lower Shiré) as constituents of the fauna of Lake Nyasa. Dealing with the records in this sense, therefore, fishes have been described as endemic in Victoria Nyanza when they have been taken in the Victoria Nile as well as in the lake itself, or even should they have been obtained only from the Victoria Nile. For Nyasa and the Upper Shiré the same principle is adopted. In a few cases also, fishes taken within the obvious drainage area of a lake are included in the list, as it would clearly be illogical to omit them. All the instances, however, in which records are not actually from the lakes themselves, are specially indicated by a §.

* Throughout this paper, wherever a tabular form has been adopted, an E is used to indicate that the species referred to is endemic; P, that it is present in the lake named but known elsewhere. Gen. E implies that the genus is endemic.

§ Not actually recorded from the lake itself. See footnote above.

‖ This record needs confirmation.

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Kivu.	Other parts of the world.
Family Cyprinidæ.							
Labeo horie …………………	…	…	…	P	…	…	Nile.
„ mesops ………………	…	…	E	…	…	…	Upper Shiré R.
„ victorianus ………	…	E	…	…	…	…	Victoria Nile .
„ cylindricus …………	P	…	P	…	…	…	Abyssinia to Zambezi.
Discognathus johnstonii ……	…	P	…	…	…	…	E. Africa.
Varicorhinus stappersii ……	E						
„ tanganicæ ……	E						
Barbus tropidolepis ………	E						
„ lobogenys …………	…	E					
„ kivuensis …………	…	…	…	…	…	E	
„ radcliffii …………	…	E					
„ altianalis …………	…	…	…	…	…	P	Rusisi R.
„ fergussonii ………	…	…	…	…	E		
„ bayoni ………………	…	E §	…	…	…	…	Victoria Nile.
„ eduardianus ………	…	…	…	…	E		
„ eurystomus ………	…	…	E				
„ rhoadesii …………	…	…	E				
„ platyrhinus ………	E						
„ nyassæ ……………	…	…	E				
„ johnstonii …………	…	…	E				
„ trimaculatus ………	…	…	P	…	…	…	Zambezi, Angola.
„ nummifer …………	…	P	…	…	…	…	E. Africa.
„ paludinosus ………	…	P	…	…	…	…	E. Africa, Natal, Angola.
„ thikensis …………	…	P	…	…	…	…	E. Africa.
„ serrifer ……………	P	…	…	…	…	…	Uellé R.
„ minchini …………	…	E	…	…	…	…	Malawa R.
„ tetraspilus ………	…	E					
„ sexradiatus ………	…	E					
„ litamba ……………	…	…	E				
„ apleurogramma ……	…	E					
„ innocens …………	…	…	P	…	…	…	E. Africa.
„ tæniopleura ………	E						
„ urostigma …………	E						
„ arcislongæ ………	…	…	E				
„ perince ……………	…	…	…	…	P ? ‖	…	Nile.
„ trispilopleura ……	…	P ? ‖	…	…	…	…	Abyssinia.
„ doggetti …………	…	E					
„ lufukiensis ………	E						
„ magdalenæ ………	…	E					
Barilius microcephalus………	…	…	E	…	…	…	Upper Shiré.
„ moorii ………………	P	…	…	…	…	P	
„ tanganicæ ………	E						
„ microlepis ………	…	…	E				
Engraulicypris sardella ……	…	…	E	…	…	…	Upper Shiré.
„ argenteus …	…	E					
„ minutus ……	E						
Family Siluridæ.							
Clarias anguillaris …………	…	P	…	…	…	…	Nile, Chad.
„ moorii………………	…	…	…	…	E		
„ mossambicus ………	P	P	…	…	…	…	Abyssinia, E. Africa.
„ lazera ………………	…	…	…	P	P	…	Syria, Nile, W. Africa.
„ carsonii …………	…	P	P	…	…	…	Uganda.
„ submarginatus ……	…	…	…	…	…	P	Cameroon, Ituri R.
„ liocephalus ………	P	…	…	…	…	…	Ubanghi R.
„ alluaudi …………	…	E					
„ werneri …………	…	P	…	…	…	…	Uganda.
Dinotopterus cunningtoni …	Gen. E						
Entropius niloticus ………	…	…	…	P	…	…	Nile, Senegal.
Schilbe mystus ………………	…	P	…	…	…	…	Nile, Tropical Africa.

§ Not actually recorded from the lake itself.
‖ This record needs confirmation.

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Kivu.	Other parts of the world.
Bagrus bayad	...	...	..	P	...	...	Nile, W. Africa.
,, orientalis	..	...	P	...	...	...	E. Africa.
,, docmae	P	P	...	P	...	...	Nile.
,, degeni	...	E					
,, meridionalis...........	...	..	E §	...	...	..	Upper Shiré R.
Chrysichthys sianenna	E						
,, graueri	E						
,, cranchii	P	...	...	. .	...	...	Congo.
,, stappersii	E						
,, myriodon	E						
,, grandis	E						
,, brachynema ...	E						
Phyllonemus typus	Gen. E						
Amphilius platychir	P	...	P	...	...	...	E. Africa.
Auchenoglanis occidentalis ...	P	...	...	P	...	...	Nile, W. Africa.
Synodontis granulosus	E						
,, dhonti	E						
,, zambesensis	...	...	P	...	...	...	Zambezi, E. Africa.
,, melanostictus ...	P	...	...	...	...	...	Zambezi, Bangweolo, Mwero.
,, multipunctatus ...	E						
,, victoriæ	...	E	...	...	...	...	Malawa R.
,, afro-fischeri	...	E					
,, nigrita	...	...	...	P	...	...	Nile, W. Africa.
Malapterurus electricus	P	...	...	P	...	...	Nile, Tropical Africa.
Family CYPRINODONTIDÆ.							
Fundulus tæniopygus	...	P	...	...	...	..	E. Africa.
Haplochilus dhonti	E §	...	...	...	...	...	Lukuga R.
,, pumilus	P	P					
,, johnstonii	...	...	P §	...	...	...	Nyasaland, Zululand.
Lamprichthys tanganicanus ..	Gen. E						
Family SERRANIDÆ.							
Lates niloticus	...	...	...	P	...	...	Nile, W. Africa.
,, microlepis	E						
,, angustifrons	E						
Luciolates stappersii	Gen. E						
,, brevior.............	E						
Family CICHLIDÆ †.							
Tilapia shirana	...	...	P	...	...	...	Zambezi.
,, mossambica	...	...	P §	..	...	...	E. Africa, Natal.
,, nilotica	P	...	...	P	P	P	Syria, Nile, W. Africa.
,, eduardiana	...	P §	..	...	P §	...	E. Africa.
,, variabilis	...	E	...	...	...	...	Victoria Nile.
,, auromarginata	...	...	E				
,, squamipinnis	...	...	E	...	...	...	Upper Shiré.
,, melanopleura	P	...	P	...	...	P	W. Africa, Zambezi, Zululand.
,, burtoni	P	...	...	...	...	P	
,, adolphi-frederici	...	...	...	...	...	E	
,, calliptera	...	...	P	...	...	...	Zambezi.
,, williamsii	...	...	E				
,, horii	E						

---

§ Not actually recorded from the lake itself.

† Quite recently, and since this section on the Pisces was completed, an important paper dealing with the classification of the Cichlids has been published by Regan (**145**). Entering on a revision of the fishes of this group, he deals in this introductory article with the Tanganyika genera. Since he has not yet completed his investigations, I have not attempted to revise my list in accordance with his views, and merely call attention to the paper in this place. It is clear that in this tabulation I am compelled to conform to the standard originally adopted, which cannot be brought into line with the suggestions put forth in the above-mentioned preliminary essay.

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Kivu.	Other parts of the world.
Tilapia perrieri	...	E					
„ humilior	...	E					
„ pallida	...	E					
„ pappenheimi	...	...	...	...	E		
„ lacrimosa	...	P	...	...	P	...	Victoria Nile.
„ nubila	...	E	...	...	...	...	Victoria Nile.
„ macrops	...	P	...	...	P		
„ martini	...	P	...	...	P		
„ bayoni	...	E §	...	...	...	...	Victoria Nile.
„ nigricans	...	E	...	...	...	...	Victoria Nile.
„ simotes	...	E §	...	...	...	...	Victoria Nile.
„ zebra	...	...	E				
„ aurata	...	...	E				
„ pleurotaenia	E	...	...	...	...	...	Rusisi R.
„ johnstonii	...	...	E				
„ tetrastigma	...	...	P	...	...	...	Nyasaland.
„ kirkii	...	...	P	...	...	...	Nyasaland.
„ lateristriga	...	...	E				
„ lethrinus	...	...	E				
„ rostrata	...	...	E				
„ dardennii	E						
„ macrophthalma	...	...	E				
„ brevis	...	...	E				
„ inornata	...	...	E				
„ trematocephala	E						
„ boops	E						
„ grandoculis	E						
Petrochromis tanganicae	E						
„ andersonii	P	...	...	P? ‖			
„ polyodon	E						
„ nyassae	...	...	E				
„ fasciolatus	E						
Cunningtonia longiventralis	Gen. E						
Simochromis diagramma	Gen. E						
Tropheus moorii	Gen. E						
„ annectens	E						
Asprotilapia leptura	Gen. E						
Lobochilotes labiatus	Gen. E						
Docimodus johnstonii	...	...	Gen. E §	...	...	...	Upper Shiré.
Haplochromis livingstonii	...	...	E	...	...	...	Upper Shiré.
„ venustus	...	...	E				
„ schubotzi	...	...	...	...	E		
„ muchisquamulatus	...	E					
„ jeanneli	...	E					
„ angustifrons	...	...	...	...	P	P	
„ ishmaeli	...	E	...	...	...	...	Victoria Nile.
„ roberti	...	E					
„ stanleyi	...	E	...	...	...	...	Victoria Nile.
„ percoides	...	E	...	...	...	...	Victoria Nile.
„ graueri	...	...	...	...	P	P	
„ strigigena	...	...	...	P	...	P	Nile, E. Africa.
„ desfontainesii	P	P	...	P	...	P	Syria, Nile, Tunisia.
„ alluaudi	...	E	...	...	...	...	Victoria Nile.
Paratilapia gestri	...	E	...	...	...	...	Victoria Nile.
„ parvidens	...	E §	...	...	...	...	Victoria Nile.
„ pfefferi	E						
„ afra	...	...	E				
„ modesta	...	...	E	...	...	...	Upper Shiré.
„ thumbergii	...	...	P	...	...	...	Zambezi, Bangweolo, [Angola.
„ vittata	...	...	...	...	...	E	
„ compressiceps	...	...	E				
„ longirostris	...	E	...	...	...	...	Victoria Nile.
„ prognatha	...	E	...	...	...	...	Victoria Nile.

---

§ Not actually recorded from the lake itself.
‖ This record needs confirmation.

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Kiva	Other parts of the world.
Paratilapia serranus	...	P	...	...	P	...	Victoria Nile.
„ guiarti	...	E	...	...	...	...	Victoria Nile.
„ bayoni	...	E	...	...	...	...	Victoria Nile.
„ chilotes	...	E §	...	...	...	...	Victoria Nile.
„ pectoralis	...	E §	...	...	...	...	Victoria Nile.
„ maculipinna	...	E					
„ victoriana	...	E	...	...	.	...	Victoria Nile.
„ granti	...	E					
„ cinerea	...	E					
„ crassilabris	...	E	...	...	...	...	Victoria Nile.
„ bicolor	...	E	...	...	..	...	Victoria Nile.
„ retrodens	...	E	...	...	...	...	Victoria Nile.
„ polyodon	...	E	...	...	...	...	Victoria Nile.
„ nototaenia	...	...	E				
„ dimidiata	...	...	E	...	...	...	Upper Shiré.
„ rhoadesii	...	...	E				
„ chrysonota	...	...	E				
„ intermedia	...	...	E				
„ ventralis	E						
„ dewindti	E						
„ lukugae	E §	..	...	...	...	...	Lukuga R.
„ furcifera	E						
„ stenosoma	E						
„ microlepis	E						
„ leptosoma	E						
„ nigripinnis	E						
„ calliura	E						
Pelmatochromis polylepis ...	E						
„ riponianus ..	...	E §	...	...	...	...	Victoria Nile.
„ microdon ...	...	E					
„ obesus	...	E					
„ auritus	E						
„ spekii	...	P	...	...	P	...	Victoria Nile.
„ flavipinnis ..	...	E					
„ cavifrons ...	...	E	...	...	..	...	Victoria Nile.
„ frontosus ...	E						
„ macrops ...	E						
„ stappersii ...	E						
„ pleurospilus	E						
„ rhodostigma	E						
Platytaeniodus degeni	...	Gen. E					
Champsochromis caeruleus ..	...	...	Gen. E				
„ longiceps ...	...	...	E	...	...	...	Upper Shiré.
„ esox	...	...	E				
Bathybates graueri	Gen. E						
„ ferox	E						
„ horni	E						
„ vittatus	E						
„ fasciatus	E						
„ minor	E						
Haplotaxodon microlepis......	Gen. E						
Cyrtocara moorii	...	...	Gen. E				
Ectodus descampsii	Gen. E						
Enantiopus melanogenys ...	Gen. E						
„ ochrogenys	E						
„ ? albini	E						
Stappersia singularis	Gen. E						
Xenotilapia sima	Gen. E						
„ ornatipinnis	E						
Grammatotria lemairii........	Gen. E						
Trematocara marginatum ...	Gen. E						
„ nigrifrons	E						
„ unimaculatum...	E						
Gephyrochromis moorii	Gen. E						

§ Not actually recorded from the lake itself.

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Kivu.	Other parts of the world.
Lamprologus brevianalis	E						
" tetracanthus	E						
" marginatus	E						
" dhonti	E						
" tretocephalus	E						
" hecqui	E						
" multifasciatus	E						
" modestus	E						
" mondabu	E						
" ? steindachneri	E						
" ? boulengeri	E						
" elongatus	E						
" pleurostigma	E						
" cunningtoni	E						
" lemairii	E						
" callipterus	E						
" fasciatus	E						
" brevis	E						
" moorii	E						
" compressiceps	E						
" tæniurus	E						
" calliurus	E						
" reticulatus	E						
" furcifer	E						
Julidochromis ornatus	Gen. E						
" ? ocellatus	E						
Telmatochromis temporalis	Gen. E						
" vittatus	E						
Bayonia xenodonta	...	Gen. E §	...	...	..	...	Victoria Nile.
Hemitilapia oxyrhynchus	...	...	E				
" bayoni	...	E	...	...	...	...	Victoria Nile.
" materfamilias	...	E					
Corematodus shiranus	...	...	Gen. E §	...	...	...	Upper Shiré.
Eretmodus cyanostictus	Gen. E						
Spathodus erythrodon	Gen. E						
Perissodus microlepis	Gen. E						
Chilotilapia rhoadesii	...	...	Gen. E				
Schubotzia eduardiana	...	...	...	...	Gen. E		
Xenochromis hecqui	Gen. E						
Plecodus paradoxus	Gen. E						
Family ANABANTIDÆ.							
Anabas muriei	.	P	...	...	...	...	Nile.
Family MASTACEMBELIDÆ.							
Mastacembelus frenatus	E						
" cunningtoni	E						
" moorii	E						
" shiranus	...	...	E	...	...	...	Upper Shiré.
" victoriæ	..	E	...	...	...	...	Victoria Nile.
" ellipsifer	E						
" mellandi	P §	...	...	...	...	...	N. Rhodesia.
" tæniatus	E						
" tanganicæ	E						
" ophidium	E						
12 families	11	9	7	6	4	3	
72 genera	26E,29P. (55)	2E,23P. (25)	5E,20P. (25)	14P.	1E,7P. (8)	6P.	
308 species	121E.25P. (146)	60E,26P. (86)	43E,20P. (63)	17P.	6E,12P. (18)	3E,10P. (13)	

§ Not actually recorded from the lake itself.

It is evident that a table which enumerates 308 species and extends over several pages is far too unwieldy to convey a correct impression of the outstanding features of distribution. The principal table of distribution is therefore supplemented by two tabular lists, which will serve as a summary and at the same time emphasise the points which are most striking. The first supplementary table supplies the number of species represented in each lake classified under their respective families.

Number of Species represented in Lakes.

Name of Family.	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Kivu.
Polypteridæ ……	1 P	…	…	1 P		
Lepidosirenidæ …	1 P	1 P	…	…	1 P	
Mormyridæ ……	2 P	2 E 3 P	4 P			
Clupeidæ ………	2 E					
Characinidæ … .	2 E 3 P	2 E 1 P	1 P	3 P		
Cyprinidæ ………	9 E 3 P	11 E 5 P	10 E 3 P	1 P	2 E 1 P	1 E 2 P
Siluridæ …………	11 E 8 P	4 E 6 P	1 E 4 P	7 P	1 E 1 P	1 P
Cyprinodontidæ…	2 E 1 P	2 P	1 P			
Serranidæ ………	4 E	…	…	1 P		
Cichlidæ …………	84 E 5 P	40 E 7 P	31 E 7 P	1 P	3 E 9 P	2 E 7 P
Anabantidæ ……	…	1 P				
Mastacembelidæ ..	7 E 1 P	1 E	1 E			
308 species …	121 E 25 P. (146)	60 E 26 P. (86)	43 E 20 P. (63)	17 P.	6 E 12 P. (18)	3 E 10 P. (13)

The other supplementary list simply gives the number of endemic genera known from the lakes in question arranged according to families.

Number of Endemic Genera in Lakes.

Name of Family.	Tanganyika.	Victoria Nyanza.	Nyasa.	Edward Nyanza.
Clupeidæ ………………	1			
Siluridæ ………………	2			
Cyprinodontidæ ………	1			
Serranidæ ………………	1			
Cichlidæ ………………	21	2	5	1
5 families ………	26	2	5	1

It is clearly impossible to allude specifically to more than a few of the points of interest which emerge from a study of the preceding tables. Many details of lesser importance will be found discussed in the various papers on the fresh-water fishes of Africa mentioned in the bibliography or in the British Museum Catalogue (36). Attention must, however, be drawn to the most significant features, many of which are now brought into special prominence by means of the tabular method employed.

The point that first arrests attention is that Tanganyika contains no fewer than 146 different forms of fish, which is in itself a remarkable number to come from within the bounds of a single lake. The fact becomes still more striking by a comparison with Victoria Nyanza which contains 86 forms, and Nyasa which contains 63. Thus, Tanganyika has more than half as many species again as Lake Victoria and over twice as many as Nyasa, and this despite the fact that Victoria is a bigger lake than Tanganyika and Nyasa not much inferior to it in size.

It must next be observed that of the 146 species known from Tanganyika, no less than 121 are peculiar to that lake, while in comparison 60 out of 86 are endemic in Victoria Nyanza and 43 out of 63 in Nyasa. That is to say, nearly 83 per cent. of the fish of Tanganyika are found in that lake alone, while of the species found in Victoria Nyanza, 69 per cent. are peculiar to the lake and in Nyasa 67 per cent. Tanganyika, indeed, contains more than double as many endemic species as Lake Victoria, which shows the next largest total.

Although the number of endemic species in Tanganyika is clearly remarkable, the number of endemic genera is still more so. Of the 55 genera known to occur there, nearly half (26) are found in that lake alone. A comparison with the two other lakes, as instituted above, serves to emphasise the exceptional nature of this fact. Two genera only out of 25 are endemic in Victoria Nyanza and five out of 25 in Nyasa. The number of genera recorded from Tanganyika forms a remarkably large proportion of the total enumerated in the table of distribution. A comparison of the figures shows that whereas this lake contains 146 species out of a grand total of 308, *i. e.* 47 per cent., it contains 55 genera out of 72—no less than 76 per cent.

It will now be well to review the list of fishes in rather more detail, dealing in general terms with the various families and the distribution of their representatives in the lakes. There is little to comment on as far as the Polypteridæ and Lepidosirenidæ are concerned. Species of *Polypterus* and *Protopterus* are fairly well represented in the big lakes, but the details of their distribution have no particular significance.—Of the Mormyridæ no species have as yet been obtained from the smaller lakes, and the family has but few forms in the three bigger ones. Only Victoria Nyanza contains endemic species.—It is interesting to note that the Clupeidæ are to be found in Tanganyika alone, where there is an endemic species of the fresh-water genus *Pellonula*, as well as a representative of a closely allied endemic genus.—A few forms of Characinidæ occur in the bigger lakes, of which Tanganyika and Victoria each contain two types peculiar to themselves.

The family Cyprinidæ is better represented than the others hitherto considered, but this is mainly due to the number of species of the very widely distributed genus *Barbus*, of which about 250 forms have been already described from the fresh-waters of Africa. There are types of this genus peculiar to each of the lakes under review with the exception of Lake Albert, in which, strange to say, no representative has yet been found. The genus *Varicorhinus*, found in Asia and various parts of Africa, occurs in the lakes only in Tanganyika, where there are two characteristic species. It is noteworthy of the genus *Engraulicypris* that each of the three big lakes appears to contain a form peculiar to itself.

The family Siluridæ cannot be expected to afford evidence of much value concerning geographical distribution, since many of its members can remain for prolonged periods out of water and even progress for some distance over land. There are therefore few points of significance to which attention need be drawn, but it may be pointed out that even in this group, Tanganyika exhibits two endemic genera. Further, it is curious to note that the genus *Chrysichthys*, while common in the Nile and Tropical Africa, occurs in Tanganyika alone, in which six of the seven species named are likewise endemic.

Only a few types of the family Cyprinodontidæ are represented in the list, but among them is *Lamprichthys*, a genus peculiar to Tanganyika.—The genera *Lates* and *Luciolates* are the only members of the Serranidæ to be found in the big lakes, and of the species which occur, only one—the well-known *Lates niloticus*—appears outside the confines of Tanganyika. Thus in this group also there is a genus (*Luciolates*) endemic in that lake.

While the families hitherto considered show various noteworthy features of distribution, it is the Cichlidæ which far surpasses them all, both in interest and in the number of forms represented in the African lakes. Of all the species enumerated in the table of distribution, more than 70 per cent. are Cichlids, or to put it another way, there are considerably more species of the family Cichlidæ than of all the other families taken together. In the case of the genera, exactly half are Cichlids, there being 36 out of a total of 72. These are remarkable facts, but they are not merely an expression of the common occurrence of this group of fishes on the continent, as an examination of the list will show. It is quite clear that there are groups of forms which are peculiar to these big lakes, and that the three biggest contain more than the smaller ones, while a culminating point is reached in Tanganyika with a succession of endemic genera.

Lake Albert is alone in containing no endemic species, but the numbers grow from 2 and 3 endemic forms in Lakes Kivu and Edward respectively, to 31 in Nyasa, 40 in Victoria Nyanza, and no less than 84 in Tanganyika. Nor is this all, for in the number of endemic Cichlid genera the remarkable nature of the fauna of Tanganyika is particularly exemplified. In the latter lake 21 peculiar genera occur, as compared with 2 in Lake Victoria, 5 in Nyasa, and a single genus in Lake Edward. As concerns Tanganyika, the case may be stated even more forcibly by pointing out that 41 genera in all are recognised from the whole continent, of which 21 belong exclusively to this lake: in other words more than half the genera of Cichlidæ known in Africa are confined within the limits of Tanganyika.

It may be worth while to give a few more comparative figures in the case of the three bigger lakes around which interest principally centres. In Nyasa 38 Cichlid fishes are found out of a total fish fauna of 63, which is 60 per cent. of the whole; in Victoria Nyanza 47 out of 86, which is some 54 per cent.; in Tanganyika 89 out of 146, or nearly 61 per cent. of the total. With this remarkable total of 89 Cichlid fishes, Tanganyika, in fact, establishes another record, possessing the richest Cichlid fauna in the world. Next note how extremely large a proportion of the endemic species are Cichlidæ. In Nyasa there occur 31 endemic Cichlid species out of a total of 43 endemic species in the lake, *i.e.* 72 per cent.; in Victoria Nyanza 40 out of 60, or 66 per cent.; in Tanganyika 84 out of 121, or 69 per cent. The proportion of endemic genera belonging to this family is even more extraordinary, for all the genera which are endemic in Nyasa and in Lake Victoria are Cichlidæ (the same is true of the single endemic genus found in Edward Nyanza), and in Tanganyika there are 21 out of 26 endemic genera, or 80 per cent. Lastly, the number of endemic Cichlid forms as compared with the total number of Cichlid forms known from the lakes in question is a basis for further striking figures. Thus in Nyasa, out of 38 species of Cichlidæ, 31 are endemic, or 81 per cent.; in Victoria Nyanza, out of 47 species, 40 are endemic, or 85 per cent.; in Tanganyika, out of 89 species, 84 are endemic, or over 94 per cent.

From a consideration of all these figures it becomes very plain that the large number of unique forms characteristic of Tanganyika is especially due to a great development of the fishes of this group, and that the same is true, though in lesser degree, for Nyasa and Victoria Nyanza.

The review of so largely represented a family must of necessity be brief. The very characteristic genus *Tilapia* extends to 40 species in the list, but though some are peculiar to certain lakes, there are no very striking features of distribution to be noted. The genus *Petrochromis* appears to be mainly typical of Tanganyika, for though an endemic form occurs in Nyasa and there is a doubtful record from Lake Albert, it is not found in Victoria Nyanza or any of the other lakes considered. The case of *Haplochromis* is interesting as being, on the contrary, a genus with a single widely distributed species recorded from Tanganyika, while it is better represented in all the other lakes under review. Perhaps a more important—though unexpected—feature is the existence of *H. angustifrons* and *H. graueri* in both

Lakes Edward and Kivu and nowhere else. This is a matter of some interest, since there is evidence for believing that these two lakes, between which there is now no connection whatever, were in relatively recent times in communication with one another (*cf.* Moore, **137**, p. 89). The genus *Paratilapia* is another represented in the list by a large number of species, these being associated in groups which in most cases are peculiar to one of the three bigger lakes. *Pelmatochromis*, which is widely distributed in West Africa, occurs in Tanganyika and in Victoria Nyanza, but otherwise only in a single instance (Lake Edward) in the lakes with which this paper is concerned.

There is no occasion to refer individually to the numerous Cichlid genera which are endemic in the African lakes, the important point being that so many of them are found in Tanganyika. Attention may, however, be called to *Champsochromis* from Nyasa with three species, and *Bathybates* from Tanganyika with six, as these exhibit the greatest number of species among the different endemic genera. The genus *Lamprologus* is of considerable interest and importance, being represented by a total of 27 species from the Congo and Lake Tanganyika. It is nevertheless essentially characteristic of the latter, for 24 endemic species are recorded from the lake, while the remaining three species are peculiar to various parts of the Congo river system. The distribution of the three forms of *Hemitilapia* is quite different from anything else met with in the list, since the genus is only known from Lakes Nyasa and Victoria. A single endemic species occurs in the former lake and two endemic species in the latter.

Since the Cichlids are so pre-eminent among the fishes of Tanganyika, and indeed constitute a most striking feature of the lake fauna as a whole, it becomes necessary to refer to certain conclusions which have been drawn from a study of the anatomy of these particular forms. From various considerations, such as the number of rays, the multiple lateral lines, and the number of vertebræ, Boulenger (**20**, p. 2: **25**, p. 393) at one time regarded certain Tanganyika genera as showing features of generalisation. At a later date, however, after a further investigation into the anatomical evidence bearing on the phylogeny of the group, he arrived (**26**, p. 422: **38**, p. 43) at a different conclusion, and considers the Tanganyika genera and species as essentially specialised. This is an important pronouncement, since it brings the case of these fishes into line with most of the other animal groups under discussion, in which certain marks of specialisation are found to be characteristic of the endemic Tanganyika forms.

Passing now to the family Anabantidæ, a solitary representative (*Anabas muriei*) has been obtained from Victoria Nyanza. It is a Nilotic type, and its existence here calls for no particular comment.—The last group in the list, that of the Mastacembelidæ, is represented in Africa only by the genus *Mastacembelus* itself. Many species are known from the fresh-waters of the continent, but examples are found only in the three biggest of the lakes included in this survey. It is interesting to note that while there are single forms peculiar to Nyasa and Victoria Nyanza respectively, there are no fewer than seven endemic forms in Tanganyika. Here there is again exemplified in very typical fashion the striking nature of the Tanganyika fauna.

In his work "The Tanganyika Problem" (**137**, p. 146) Moore has pointed out that, on the whole, the number of different animal forms present in any particular African lake is definitely proportional to its size. He expressly omits, in making this statement, the so-called "halolimnic" forms which he distinguishes in Tanganyika, and deals only with what he calls the ordinary fresh-water fauna. Regarding as inadmissible the exclusion of certain forms as "halolimnic," Tanganyika will be seen to far outstrip the other lakes in the number of types represented, but with that exception, the figures undoubtedly do vary in proportion to the size. So extensive a list as that of the fishes affords an excellent opportunity for testing the general accuracy of this statement, and a comparison may be instituted not only as regards number of species, but as regards number of genera and even families. The results are not dissimilar in the three cases, as the adjoining table will show. With the exception of Tanganyika, the lakes are arranged in order of size, from the largest to the smallest of those under review.

	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Kivu.
Number of Species	146	86	63	17	18	13
„ Genera	55	25	25	14	8	6
„ Families........	11	9	7	6	4	3

Having thus emphasised from many points of view the remarkable nature of the fish fauna of Tanganyika, an examination into its significance might well follow. As however the matter merits a detailed discussion, and is moreover by no means concerned with the distribution of the fishes only, this must be deferred. In this place it is enough to indicate that the evidence points to a period of complete isolation for Tanganyika—a period which was long enough for the inhabitants of the lake to assume the characters of species, and even genera, distinct from those of the neighbouring parts of the continent. This is indeed fully borne out by a comparison of the fish fauna of Tanganyika with that of the Congo, to the drainage area of which the lake now belongs. The striking dissimilarity of the fishes of Tanganyika and the river into which it drains may be illustrated by pointing out that of 25 species non-endemic in the lake, only

14 are known also from the Congo system, and that of these about one-third are of very wide distribution, by no means characteristic of the Congo.

A few lines may now be devoted to a general survey of the fishes of the other big lakes, for the purpose of pointing out any characteristic features and affording a ground of comparison with Tanganyika. It has already been seen that Victoria Nyanza, while containing representatives of nearly as many families as Tanganyika, contains a much smaller number of species. Very few endemic genera are found in the lake, but a considerable number of endemic species occur, especially among the Cichlidæ. It may also be noted that Lake Victoria shows a larger number of Mormyrids (including two endemic types) than does Tanganyika. Again, as regards the Cyprinidæ, this lake is richer in forms, with 11 endemic species mostly belonging to the genus *Barbus*, while the Anabantidæ is represented here alone. Speaking generally it may be said, that although now one of the sources of the Nile, only a small proportion of its fish are found also in that river, so that there are good reasons for supposing that Victoria Nyanza was also isolated for a certain period, and only included in the Nile basin in times, geologically speaking, recent. Meanwhile it is clear that the modifications of form which exist are not comparable in importance to those occurring in Tanganyika, but go to prove that the lake has a peculiar fish fauna, not closely related to that of either Nile or Congo.

Nyasa, having a lesser area, shows something of that decrease in number of types which is related to the smaller size of the lake. Nevertheless it still contains more Cyprinidæ and Mormyridæ than Tanganyika, and it is relatively rich in Cichlid fishes. Of the latter there are indeed five endemic genera, yet out of a total of 38 species, 27 belong to the two genera *Tilapia* and *Paratilapia*, which are of very wide distribution. Thus, although Nyasa possesses a fish fauna which is in part peculiar and characteristic, it has a far less striking assemblage of forms than Tanganyika, or even than Victoria Nyanza. While it is probable that a period of isolation favoured the production of species peculiar to Nyasa, it is nevertheless clear that its fishes belong essentially to the Zambezi river system, and do not differ from those of that river to the same extent as do the fish of Tanganyika, and to a less degree of Victoria Nyanza, from those respectively of the Congo and the Nile.

Speaking of the fishes, it may therefore be said that each of the three largest lakes contains a group of forms peculiar to and characteristic of itself. These forms differ from the fish of the rivers which drain the lakes, but not to the same degree in each instance. Nyasa exhibits a number of types which are not found in the Zambezi, and Victoria Nyanza a larger and more divergent series of forms which are not found in the Nile; but in these cases the differences are for the most part only specific.

Tanganyika, however, is the extreme case, where not merely specific but generic distinctions occur, and a remarkable fish fauna exists which has very little in common with the fishes of the Congo, and which, moreover, has no parallel elsewhere.

Albert Nyanza is the only lake of those under review which does not contain a single endemic species of fish. The family Siluridæ is best represented, with 7 different forms, belonging to 6 different genera, but these are without exception well-known Nilotic species. Very few Cichlid fishes are found in the lake, the most interesting being *Petrochromis andersonii*, a Tanganyika type, the existence of which in Lake Albert needs confirmation. With this exception, and with the exception of *Alestes macrophthalmus*, a Congo-Tanganyika type, the occurrence of which in the lake is also rather doubtful, the whole of the fishes belong essentially to the Nile system, of which the lake is thus shown to be an integral part.

Lake Edward, which lies further south, but is similarly in direct connection with the Nile, is nevertheless not without types peculiar to itself. Two endemic speces of *Barbus* have been described, and one of *Clarias*. The Cichlidæ are well represented here with 12 forms, 3 of which, including the genus *Schubotzia*, are endemic. While the greater number of the fishes are either Nilotic types or are peculiar to the lake, there is a series of 6 Cichlids which are common to Lakes Edward and Victoria and are not found elsewhere. This is a rather unexpected state of affairs, and it is by no means easy to account for the association, since the lakes do not communicate in any way. It may be noted that in Lake Edward the total number of genera is reduced to eight and the number of families to four.

Dealing lastly with Lake Kivu, the smallest lake is seen to contain the smallest number of different species of fish. Yet even here an endemic species of *Barbus* and two endemic Cichlids occur. Apart from these, the fish fauna gives indications of being considerably mixed. Three species belong clearly to the Nile group, while reference has already been made to the two forms of *Haplochromis* found in Lakes Kivu and Edward only. On the other hand, two fishes are found in Kivu and Tanganyika only: a third occurs in Tanganyika and the Rusisi River which drains Lake Kivu, as well as in the lake itself. The two remaining types have a wider distribution, extending into West Africa.

In works dealing with Geographical Distribution it has long been recognised that undoubted affinities exist between the animals of Southern Asia—and of the Indian Peninsula in particular—and of East and Central Africa. While evidence of this is more marked in some groups than in others, clear testimony as to the general truth of the assertion is to be gained by a study of certain families of fishes. Of the families under discussion, it is pre-eminently the Cyprinidæ and Mastacembelidæ which exhibit this affinity in a striking degree. Among the Cyprinidæ, various genera are common to India and Africa, and a close relationship is sometimes recognisable even between species. The genera found in the African lakes which best exemplify this relationship, are *Labeo*, *Discognathus*, and *Barbus* (of the group allied to *Barbus bynni*). *Mastacembelus* itself is the only genus of the Mastacembelidæ which occurs in Africa, but it is also well represented in India and the Malay Archipelago. This case is specially interesting, since the genus was at one time considered quite characteristic of the Indian region, yet at the present day an even larger number of forms is known from the continent of Africa.

Summary.—The lakes of Central Africa contain a large and interesting assemblage of fishes. The bigger lakes as a rule possess more forms than the smaller, but while Nyasa and Victoria Nyanza each possess an extensive fish fauna, Tanganyika can show a far larger number of types. In Nyasa and Lake Victoria a considerable percentage of these types are endemic, but this is more strikingly the case in Tanganyika, where indeed not merely endemic species, but a very exceptional number of endemic genera are found. Of the 12 families which are represented, interest centres in particular on the Cichlidæ, which are very prominent in all the lakes except Albert Nyanza. A large proportion of the Cichlid species are endemic in the lakes where they occur, the extreme case being that of Tanganyika, which, with 84 endemic species and 21 endemic genera, possesses the richest Cichlid fauna in the world. There are reasons for believing that these remarkable endemic Cichlidæ show signs of specialisation. An explanation of the unique fish fauna of Tanganyika is probably to be found in a period of complete isolation of that lake: it is possible that isolation for a lesser period has produced an effect in the cases of Victoria Nyanza and Nyasa. The fishes of the families Cyprinidæ and Mastacembelidæ in particular exhibit indications of Afro-Indian affinities such as are displayed by other groups of organisms.

POLYZOA.

The representatives of this group, as far as Lake Tanganyika is concerned, are of particular interest. This is due in the first place to the fact that while examples of the Phylactolæmata were quite to be expected, the latter are accompanied in Tanganyika by two species of Gymnolæmata, the members of which are, with few exceptions marine. It is also true that the gymnolæmatous form which was first discovered by Moore (**137**, p. 295) has a remarkable resemblance to the marine genus *Arachnidium*. With the exception of this type, which Moore named *Arachnoidea* *, the species from Tanganyika were all obtained for the first time by the author during the Third Tanganyika Expedition.

---

* I follow Annandale (**7**, p. 198) and Harmer (**99**, p. 59) in adopting *Arachnoidea* as the correct spelling of this generic name, which Moore originally wrote *Arachnoidia*.

Table of Distribution of Polyzoa †.

Name of Species.	Tanganyika.	Victoria Nyanza.	Albert Nyanza.	Edward Nyanza.	Other parts of the world.
Order GYMNOLÆMATA.					
Victorella symbiotica	E ?	...	...	...	Birket Qarun ?
Arachnoidea ray-lankesteri ...	E				
Order PHYLACTOLÆMATA.					
Fredericella cunningtoni	E				
Plumatella repens	P	P	P	P	Cosmopolitan.
" emarginata	...	P	P	P	Cosmopolitan.
" (Afrindella) tanganyikæ ...	P	...	...	...	India.
6 species	3 E 2 P	2 P	2 P	2 P	

The above table illustrates an interesting feature of distribution, paralleled in the case of other organisms, where one or more than one almost cosmopolitan species occurs in Tanganyika, associated with a larger number of endemic forms. *Plumatella repens*, a form with a most extensive range, is represented in Tanganyika as well as in Lakes Victoria, Albert, and Edward, while the closely related *P. emarginata* is found in the latter three lakes, but has not been recorded from Tanganyika. The case of *P.* (*Afrindella*) *tanganyikæ* is of considerably more interest, for it was originally described as *P. tanganyikæ* by Rousselet (**149**, p. 252) from material collected by the Third Tanganyika Expedition. It was at that time believed to be peculiar to Tanganyika, but Annandale (**5**, p. 225) subsequently referred to this identical species, specimens which he obtained from Igatpuri Lake in the Western Ghats, Bombay Presidency *. Still more recently (**8**, p. 140) the same author established the subgenus *Afrindella* to receive the species, indicating in the name the striking feature of its distribution. The absolute identity of forms from Tanganyika and from India is a most remarkable instance of those Afro-Indian affinities to which reference has already been made ‡.

The remaining phylactolæmatous form, *Fredericella cunningtoni*, has sufficiently marked peculiarities to distinguish it from the well-known *F. sultana*, which has an almost world-wide distribution. The former is confined to Tanganyika as far as is at present known.

Among the great lakes of Central Africa, Tanganyika alone has been found to contain representatives of the Gymnolæmata.

---

† For descriptions of most of these species and remarks on distribution, see the report by Rousselet on the Polyzoa of the Third Tanganyika Expedition (**149**).

* These specimens he at first named *P. bombayensis* (**4**, p. 169)—a species afterwards discarded.

‡ A table of African and Indian Polyzoa is given by Annandale in his paper on the resemblances between African and Indian fresh-water faunas (**10**, p. 582).

The well-known genus *Victorella*, essentially a brackish and fresh-water genus, is represented by the form *V. symbiotica*, a species found associated with and growing through the sponge *Spongilla tanganyikae*. During an expedition more recently undertaken to the Birket Qarun in Lower Egypt, on which I was accompanied by C. L. Boulenger, further specimens of a gymnolæmatous Polyzoon were collected, which were submitted to Rousselet for examination. No definite report on these has been received, but some of this material has evidently been transmitted by Rousselet to other writers on the Polyzoa, for Annandale (**7**, p. 197) records his belief from an examination of the specimens, that the Qarun species is identical with *Victorella symbiotica* from Tanganyika. Braem, on the other hand (**53**, p. 33), whilst affirming that the forms *V. continentalis*, *V. bengalensis*, and that from the Qarun have close affinities with the European *V. pavida*, asserts that "Rousselets *V. symbiotica* aus dem Tanganyika . . . . durch einen abweichenden Bau des Darms ausserhalb dieses Kreises steht" (*loc. cit.* p. 34).

Be this as it may, there is a further matter concerning this genus which demands consideration. The view generally held by specialists on this group has been that *Victorella* only recently migrated from the sea into brackish and fresh-water. Braem, however (**53**, p. 34), in the light of the Qarun specimens and the species he describes from an inland lake in Turkestan, declares his belief that on the contrary the genus is one which primitively adapted itself to fresh-water conditions, and that the specimens in question are "relict" forms. He considers that the existence of the genus in Tanganyika further strengthens his supposition. Since Tanganyika has been claimed by Moore as an undoubted "Reliktensee," the true nature of this Polyzoon genus becomes a matter of some importance. Further light is fortunately shed on this problem by the recent discovery by Harmer (**99**, p. 45), in the Siboga material from the Dutch East Indies, of a truly marine species of *Victorella*. The usual view would thus seem to be definitely supported, and the existence of *V. symbiotica* in Tanganyika, while of considerable interest, would not tend to prove the occurrence in the lake of an ancient marine fauna.

The second gymnolæmatous type—*Arachnoidea ray-lankesteri*—is certainly the most remarkable form from the African fresh-waters. Despite recent discoveries, it remains one of the few instances known of a fresh-water incrusting gymnolæmatous Polyzoon, and is of peculiar interest accordingly *. In consequence of its undoubted resemblance to the marine genus *Arachnidium*, to which reference has already been made, Moore (**137**, pp. 330, 332) regarded it as an important member of that group of primitive marine forms which, he contended, still exists in Tanganyika. Quite a different conception now suggests itself, in view of the recent description by Harmer (**99**, p. 50) of another species belonging to this genus collected by the Siboga Expedition in the Straits of Makassar. No one would have ventured to predict that Moore's genus would be found to have a representative still living in the sea, but the discovery shows that, as in the case of *Victorella*, the Tanganyika species has affinities with a present-day marine type and not problematical affinities with marine Polyzoa of a past era. It may be pointed out that a further instance of Afro-Indian associations is afforded by the finding of this species of *Arachnoidea* in East Indian seas.

---

* Another genus is *Hislopia*.

A piece of negative evidence of some interest, but to which perhaps no great importance need be attached, is the apparent absence of Polyzoa from Lake Nyasa. It is admittedly a fact that these organisms are small and inconspicuous, and little likely to attract the attention of any but skilled naturalists; moreover, their distribution in the African lakes has in some cases been merely deduced from a discovery of their sessile statoblasts. On the other hand, Nyasa has received a considerable amount of attention from a trained observer in the person of Prof. Fülleborn, and it is certainly strange that (so far as I am aware) he collected no representatives of this group from that lake.

Polyzoa are also unknown in Kivu, where Schubotz states he was unable to discover them (**156**, p. xiv). This is less surprising on account of the unusual salinity of the lake.

MOLLUSCA.

It is a task of exceptional difficulty to give an accurate account of the molluscan fauna of the big lakes. This is in a large measure due to the work of the late J. R. Bourguignat, who described a very large number of types, a considerable but varying proportion of which have not been accepted by other authorities. From Tanganyika alone, Bourguignat described no less than 242 species *, and to this total must be added a number of species for which other writers are responsible, yet in the opinion of some of the principal specialists the number of different molluscan forms living in that lake is very much smaller than the enormous total which has been credited to it.

The great interest attaching to certain Tanganyika molluscs owing to their remarkable marine-like appearance has already been referred to, and on account of this, it is the more to be regretted that both genera and species have been unduly multiplied and that a generally accepted list of forms from this lake is not available. In writing a paper such as this, it is necessary to compile a definite list, and in doing so, I have followed more particularly the account given by Edgar Smith (170), who had an unusual opportunity for the systematic study of African fresh-water shells.

---

* Speaking generally it may be said that Bourguignat and his school, of which Locard was the principal exponent, elevated species into groups, and varieties into species.

To a lesser degree, the "species making" of Bourguignat has affected the lists of mollusca from the other big lakes of Africa, and in making a selection of forms to be retained and forms to be rejected, I have no doubt acted arbitrarily. There is no need to enlarge upon this point, but while all the lists have been carefully considered with a view to the elimination of synonyms, they must be taken merely as the writer's expression of opinion. It is only necessary to emphasise that while finality in such a matter is always impossible, it is especially so in the case of the Mollusca.

Although the number of genera and species to be included in the fauna of Tanganyika may be a matter of opinion, there are certain striking facts which remain undisputed. Firstly, it is only among the Gasteropods that species described as thalassoid are to be met with; that is to say, all the Lamellibranchs are non-thalassoid. Secondly, while there are a number of non-thalassoid Gasteropods known to live in the lake, there are more than twice as many which are considered to show a thalassoid aspect.

The arrangement of the families and genera which has been adopted is, in the main, that given by Pelseneer (Treatise on Zoology, Ed. by Lankester, Part V. Mollusca).

Gasteropoda.

It has more than once been emphasised that the Gasteropoda are among the most remarkable of the peculiar animal forms which inhabit Tanganyika. In the adjoining table of distribution, a list is given for each of the lakes under review, of those species which appear to be admissible. This list reaches a total of 133 in all, and it is evidence of the unique position which Tanganyika holds, that 84 of these forms are recorded from that lake, 76 of them being unknown elsewhere. Of these endemic Tanganyikan species, the great majority were described by Bourguignat and others as thalassoid and alternatively by Moore as halolimnic (*cf.* p. 517). It has been thought desirable, in view of the special interest attaching to these types, to mark with a * all the genera which have been so designated. Perhaps it is well to explain that none of the species belonging to genera which occur elsewhere have been described as thalassoid by the conchologists, though this does not mean that all the endemic genera are necessarily thalassoid in aspect, there being a notable exception in the case of the genus *Neothauma*.

Table of Distribution of Gasteropoda †.

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Kivu.	Other parts of the world.
Family Viviparidæ.							
Viviparus constrictus	...	E					
,, costulatus	...	E					
,, foai	E						
,, meta	...	E					
,, rubicundus	..	P	...	P	...	...	R. Nile.
,, unicolor	...	P	P	P	P	...	Egypt, E. Africa.
,, ? brincatianus	E						
Neothauma tanganyicense	Gen. E						
Cleopatra emini	...	...	...	E			
,, guillemeti	P	P	...	...	...	...	E. Africa.
,, jouberti	E						
,, pirothi	...	...	...	P	...	...	E. Africa, Abyssinia.
,, trisulcata	E						
*Bridouxia giraudi	Gen. E						
Family Ampullariidæ.							
Ampullaria bridouxi	E						
,, gordoni	...	E					
,, gradata	...	...	P	...	...	...	E. Africa ?
,, letourneuxi	...	P	...	...	...	...	E. Africa.
,, nyanzæ	...	E					
,, ovata	P	P	P	...	P	...	Egypt, E. Africa.
,, speciosa	...	P	...	P	...	...	E. Africa.
,, stuhlmanni	...	...	...	P	P	...	E. Africa.
Lanistes ellipticus	...	...	P	..	...	...	E. Africa.
,, jouberti	E						
,, nyassanus	...	...	P	...	...	...	Nyasaland.
,, olivaceus	...	...	P	...	...	...	E. Africa.
,, ovum	...	...	P	...	...	...	E. Africa.
,, purpureus	...	...	P	...	...	...	E. Africa.
,, schweinfurthi	..	E					
,, sinistrorsus	P		...	...	...	...	E. Africa.
*Leroya bourguignati	Gen. E						
Family Hydrobiidæ.							
*Spekia zonata	Gen. E						
*Tanganyicia rufofilosa	Gen. E						
*Rumella neritinoides	Gen. E						
*Stanleya giraudi	Gen. E						
,, rotundata	E						
,, smithiana	E						
*Limnotrochus thomsoni	Gen. E						
*Chytra kirkii	Gen. E						
Bithynia alberti	...	...	...	P	P		
,, humerosa	...	P	P	...	P		
,, multisulcata	E						
,, stanleyi	...	...	E				
,, walleri	...	...	...	E			
*Syrnolopsis carinifera	Gen. E						
,, lacustris	E						

† Additional particulars and bibliographies will be found in von Martens' account of East African forms (**116**) and Smith's review of the Mollusca of Tanganyika (**170**). There have been but few additions since the dates of these papers.

* Genera described as thalassoid.

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Kivu.	Other parts of the world.
Family Tiaridæ.							
Tiara[‖] admirabilis	E						
,, arcuatula	...	...	E				
,, liricincta	...	...	...	E			
,, nodicincta	...	...	P	...	...	...	Angoni Land.
,, nyassana	...	...	E				
,, pergracilis	...	...	E				
,, polymorpha	...	...	E				
,, pupiformis	...	...	E				
,, simonsi	...	...	E				
,, tanganyicensis	E						
,, tuberculata	P	P	P	P	P	P	India, Malay Pen.
,, turritispira	...	...	E				
*Giraudia foai	Gen. E						
,, grandidieriana	E						
,, horei	E						
,, lavigeriana	E						
,, minor	E						
,, præclara	E						
,, quintana	E						
,, tanganyicensis	E						
*Lechaptoisia ponsonbyi	Gen. E						
*Burtonilla terebriformis	Gen. E						
*Baizea giraudi	Gen. E						
,, leucoraphe	E						
*Anceya admirabilis	Gen. E						
,, giraudi	E						
,, rufocincta	E						
*Bythoceras iridescens	Gen. E						
,, minor	E						
*Paramelania bridouxi	Gen. E						
,, crassigranulata	E						
,, damoni	E						
*Joubertia baizeana	Gen. E						
,, spinulosa	E						
,, stanleyana	E						
*Lavigeria callista	Gen. E						
,, combsa	E						
,, coronata	E						
,, diademata	E						
,, grandis	E						
,, jouberti	E						
,, perexima	E						
,, ruellaniana	E						
*Randabelia catoxia	Gen. E						
,, hamyana	E						
*Edgaria bourguignati	Gen. E						
,, crassilabris	E						
,, lechaptoisi	E						
,, nassa	E						
,, paucicostata	E						
,, reymondi	E						
,, singularis	E						
,, tiarella	E						
,, variabilis	E						
*Hirthia globosa	Gen. E						
,, littorina	E						
Family Tiphobiidæ.							
*Tiphobia horei	Gen. E						
*Bathanalia howesi	Gen. E						

---

* Genera described as thalassoid.

[‖] Olim *Melania*.

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Kivu.	Other parts of the world.
Family LIMNÆIDÆ.							
Limnæa natalensis	P	P	P	...	...	...	Natal.
„ nyansæ	...	E					
„ undussumæ	...	P	...	...	P	...	E. Africa.
Isidora coulboisi	E						
„ forskali	...	P	...	...	...	...	Egypt, Natal, [Angola.
„ nyassana	...	...	E				
„ randabeli	E						
„ strigosa	...	P	...	...	...	...	E. Africa.
„ succineoides	...	...	E				
„ transversalis	...	E					
„ trigona	...	E					
Physopsis africana	...	...	P	...	...	...	E. Africa, Natal.
„ ovoidea	...	P	...	...	...	...	E. Africa.
„ tanganyicæ	E						
Family PLANORBIDÆ.							
Planorbis adowensis	P	...	...	...	...	...	Abyssinia.
„ alexandrina	P	...	P	...	...	...	Egypt.
„ apertus	...	...	...	...	E		
„ bridouxiana	E						
„ choanomphalus ...	...	P	...	...	P	P	
„ crawfordi	...	P	...	...	...	...	Cape Colony.
„ gibbonsi	...	P	...	P	...	...	E. Africa.
„ lamyi	E						
„ lavigerianus	E						
„ monceti	E						
„ stanleyi	...	...	...	E			
„ sudanicus	P	P	...	P	P	...	R. Nile.
„ victoriæ	...	E					
Family ANCYLIDÆ.							
Ancylus stuhlmanni	...	E					
„ tanganyicensis	E						
8 families	1E,7P.	7 P.	6 P.	5 P.	6 P.	2 P.	
35 genera	24E,11P. (35)	11 P.	9 P.	6 P.	6 P.	2 P.	
133 species	76E,8P. (84)	11E,17P. (28)	10E,14P. (24)	4E,9P. (13)	1E,9P. (10)	2 P.	

A list such as this, with 133 species, requires a somewhat detailed analysis to bring out the points of most interest and importance, although, indeed, the tabular form reveals the exceptional nature of the Gasteropod fauna of Tanganyika. In the first place it will be noticed that no less than 84 species are recorded from Tanganyika, which is clearly an exceptional number. That this is so, is shown by a comparison with the known fauna of the two lakes which come nearest in size, for Victoria Nyanza can muster but 28 forms and Nyasa only 24. Thus Tanganyika contains three times as many Gasteropods as Lake Victoria and more than three times as many as Nyasa.

Secondly, be it observed, that of the 84 Tanganyika species, no fewer than 76 are endemic, while correspondingly only 11 out of 28 are peculiar to Victoria Nyanza and 10 out of 24 to Nyasa.

Of the smaller lakes, Albert Nyanza has 4 endemics out of a total of 13, Edward Nyanza 1 out of 10, while Kivu only contains two species, neither of which is endemic. In other words, more than 90 per cent. of the forms in Tanganyika are only known from that lake, while Victoria Nyanza has 39 per cent. of endemic species and Nyasa some 41 per cent.

In the next place it must be emphasised once more that the greater number of the endemic species of Tanganyika are types which have been described as thalassoid—58 out of 76 belonging to that category. Thus there are more than three times as many thalassoid as non-thalassoid endemic species, actually some 76 per cent. having this characteristic appearance. Even when the non-endemic forms are added to swell the total, the shells having this marine aspect outnumber the normal series by more than two to one, there being respectively 58 and 26 species.

The figures which refer to the genera are even more arresting than those which have been dealt with. Tanganyika alone contains one or more representatives of each of the 35 genera named in the table. The number of genera represented in Lake Victoria sinks to 11, but it is significant that this is due to the absence from that lake of the large total of 24 genera which are peculiar to Tanganyika. Of this total of 24, 23 are regarded as thalassoid, the single exception being the genus *Neothauma*, as already mentioned. Apart from these endemic genera, both Tanganyika and Victoria contain species belonging to the same 11 genera—those of the "normal African fresh-water fauna" to adopt Moore's term. It is interesting to observe that while 28 species of these less specialised genera (including 11 endemics) occur in Victoria Nyanza, 25 (including 17 endemics) are found in Tanganyika. Lake Nyasa with 9 of these ordinary fresh-water genera comes next, and the other lakes follow with still smaller numbers. No endemic genera are to be observed outside Tanganyika. It is thus clear that over and above the representatives of certain well-known fresh-water genera, there is, in Tanganyika, a whole series of unique Gasteropods which are not represented elsewhere.

It may not be unprofitable to institute a comparison with the group of the fishes, in which alone so large a number of endemic genera is known. Tanganyika contains 25 endemic genera of fishes, as compared with 24 endemic genera of Gasteropods, but whereas with the fishes there are in addition 29 non-endemic genera represented, there are only 11 non-endemic genera of Gasteropods. Again, among the fishes there are a few endemic genera found in the remaining lakes, while this is not the case with the Gasteropods. The comparison serves to show that while the actual numbers both of genera and species are less in the group now under discussion than in that of the fishes, it affords quite as conspicuous an instance of the peculiar characters of the Tanganyika fauna.

The table of distribution already furnished now calls for more detailed examination. Among the Viviparidæ, *Viviparus* itself is represented in Tanganyika only by two (one doubtful) endemic forms. In Lake Victoria there is a series of 5 forms, 3 of which are peculiar to its waters. It is noteworthy that the widely distributed species *V. rubicundus* and *V. unicolor* have not been obtained from Tanganyika. The genera *Neothauma* and *Bridouxia* are of more interest, since they are entirely confined to Tanganyika. The latter genus has been regarded as exhibiting a thalassoid facies. Each is represented by only a single species.

The family Ampullariidæ contains representatives of the well-known genera *Ampullaria* and *Lanistes* in addition to the thalassoid genus *Leroya* from Tanganyika. Only Victoria Nyanza and Tanganyika possess endemic forms of the two first-mentioned genera, the remaining species—especially *Ampullaria ovata*—having a wider distribution. Lake Victoria will be seen to have five species of *Ampullaria*, Nyasa a similar number of *Lanistes*. The latter genus has not been recorded from the smaller lakes.

A larger number of genera, several of great interest, are associated in the family Hydrobiidæ. *Bithynia** alone among the genera enumerated is found outside the confines of Tanganyika, but the species on record from the lakes have not been found in other parts of the continent. Of the thalassoid types, *Stanleya* is represented by 3 species and *Syrnolopsis* by 2. *Chytra* and *Limnotrochus*, as the name of the latter indicates, are forms in which the shell is suggestive of the marine genus *Trochus*.

The genera belonging to the family Tiaridæ (formerly Melaniidæ) form by far the largest assemblage in the list under consideration. Thirteen genera are represented, but here again only one of them, the type-genus *Tiara* itself (perhaps better known as *Melania*) is of wide distribution, the remainder being thalassoid forms found only in Tanganyika. The latter lake contains three species of *Tiara*, two of which are endemic; Albert Nyanza contains one endemic as well as one non-endemic species, while Nyasa contains a remarkable series of nine different types, seven of which are endemic. It is interesting to note that *Tiara tuberculata*, which has a wide range in Africa and extends into India and the Malay Archipelago, is the only one of the 133 species enumerated which occurs in all the lakes included in this survey. There is little need for comment on the remaining genera in this family. They contain the greater number of those types of marine aspect which are so remarkable a feature of the Gasteropod fauna of Tanganyika. Certain of the genera are, however, represented by quite a number of species, notably *Edgaria* by 9 species and *Giraudia* and *Lavigeria* each by 8.

Under the family name of Tiphobiidæ have been associated the genera *Tiphobia* and *Bathanalia*, which are among the most striking of the thalassoid forms from Tanganyika. At present this remains the only example of an endemic family characteristic of that lake.

---

* A species of *Bithynia* is stated by Moore (**137**, p. 129) to occur in Lake Kivu. I believe no specimens have ever reached this country, and in view of the negative evidence which the visit of the German expedition to the lake affords, I regard the record as of doubtful value and have intentionally omitted it.

The representatives of the three remaining families are all well-known fresh-water genera, and do not offer much of interest on which to comment. Of the Limnæidæ, specimens are on record only from the three large lakes and Lake Edward, which is rather surprising as the group has a wide distribution in Tropical Africa. *Limnæa natalensis* is the most widely distributed species, being known from Tanganyika, Victoria, and Nyasa, as well as from Natal. The families Planorbidæ and Ancylidæ are each represented by the type-genus only. Thirteen species of *Planorbis* are enumerated, of which Tanganyika contains the largest series, viz. 7 forms, 4 of which are endemic. In Nyasa, it is strange to note, only a single widely distributed species has been found. The form of commonest distribution in the lakes is *P. sudanicus*, which occurs in four of them as well as in the River Nile. Turning to the Ancylidæ, it will be seen that an endemic species of *Ancylus* is on record both in Tanganyika and in Lake Victoria. No specimens have been observed in the other lakes, but they may have been overlooked owing to their small size.

It is not unreasonable to refer here to the suggestion already cited in the section dealing with the fishes (*cf.* p. 535) that the number of different animal types living in a lake is directly proportional to its size. The figures for the Gasteropoda are sufficiently large to afford some evidence for this contention, and they are accordingly given in the following table, which records the number of families and genera, as well as species:—

	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Kivu.
Number of Species	84	28	24	13	10	2
„ Genera	35	11	9	6	6	2
„ Families	8	7	6	5	6	2

It will be seen that Tanganyika, with its admittedly unique fauna, is in a category by itself, but the remaining lakes, which are arranged in order of size, form a series with decreasing totals, and thus support the general truth of the assertion.

The distribution of the Gasteropoda in the lakes may be summarised in a few sentences. Tanganyika, containing 84 species, of which 76 are endemic, is altogether exceptional and is principally characterised by a remarkable series of marine-like or thalassoid forms. While the latter are not confined to one family, they belong mainly to that of the Tiaridae. Tanganyika is the only lake of those under review which contains representatives of all the genera enumerated in the table of distribution.—Victoria Nyanza, with a far smaller number of individual forms (28), can nevertheless show quite a comprehensive series of the normal fresh-water types, each of the genera being represented. The thalassoid genera and species are conspicuously absent.—Nyasa, with only slightly lower figures (24), does not differ very markedly from Lake Victoria. The genera *Cleopatra* and *Ancylus* are unrepresented, but the lake is rich in species of *Lanistes* and *Tiara*, especially the latter, of which 9 forms (7 endemic) are known.—Albert Nyanza and Edward Nyanza exhibit a progressive reduction in the number of species which they contain, but otherwise possess no outstanding features.—Lake Kivu, finally, is the extreme case, with a very reduced Gasteropod fauna. Of the two species which are known from its waters, *Tiara tuberculata* is the more widely distributed, it being in fact the only form enumerated which has been found outside the continent of Africa.

It was in the first degree the Gasteropoda which constituted Moore's argument for a halolimnic (*i.e.* relict) fauna living in Tanganyika side by side with types which are common in tropical fresh-waters. It is thus necessary to consider whether the balance of evidence is still in favour of the views regarding these Mollusca which Moore originally expressed. He held that the peculiar forms in question were essentially primitive types, and after comparisons based on their anatomy he stated:—"It is difficult, or, I may say, impossible, to view these extraordinary molluscs as either the forerunners or the derivatives of the fresh-water molluscs which we find in the lakes and rivers all over the world to-day. They are, however, readily intelligible if we regard them as the forerunners of several marine groups, such as the Strombidae, the Naticas, and the early Ciriths, to which I have referred" (**135**, p. 466).

These statements did not go by any means unchallenged, nor did the astonishing suggestion of a resemblance between some species and certain Jurassic fossil shells. Edgar Smith, in his important paper on the Mollusca of Lake Tanganyika, pointed out that Moore's conclusions were drawn from a study of only 9 out of 23 so-called halolimnic genera, adding that it became "mere conjecture" to suppose a relationship with marine forms on account of the appearance of the shell (**170**, p. 78). As an expert conchologist, Smith dealt unfavourably too with the supposed resemblances to Jurassic fossils. The matter was approached from the geologist's standpoint by Hudleston, who had made a speciality of Jurassic Mollusca (**102**). In a comprehensive paper on the origin of the halolimnic fauna of Tanganyika, he failed to find evidence of a satisfactory character in favour of Moore's views. In an appendix, Hudleston also dealt seriatim with the comparisons between living and Jurassic Gasteropods, only to reject likewise Moore's conclusions. In a discussion on this topic at the British Association Meeting in 1906 (**133**), Moore expressed less extreme views, while Pelseneer, speaking with a wider knowledge of the anatomical characters of these molluscs, asserted positively that there was no special resemblance between them and marine types and that they were no more primitive than other well-known fresh-water genera (**144**). Pelseneer added that the halolimnic Gasteropods were all to be regarded as belonging to the Melaniidæ (Tiaridæ) or families nearly akin, in which case they belong to an essentially fresh-water group. If this be indeed a fact, Moore's whole hypothesis, as far as it rested on these molluscan forms, falls to the ground. It no longer becomes necessary to speculate as to how and when Tanganyika received animal types from an ancient sea, it is sufficient to invoke prolonged isolation to account for endemic genera and species—and this is precisely what has been done in other groups.

It is true that no satisfactory explanation of the marine aspect of these Gasteropod shells is forthcoming, although certain guesses may be hazarded. Without attributing it to a direct community of descent with certain salt-water types, it might be regarded as simply due to convergence. It might be urged that the resemblance is purely accidental, or that it results from the quasi-oceanic conditions which prevail in Tanganyika. It might be due to the magnesium salts in the water, or, perhaps, to the greater degree of salinity which is believed to have formerly existed. Beyond such suggestions it is impossible to go, but it must not be overlooked that a number of fresh-water shells from other parts of the world exhibit the same characteristically marine aspect, though there may be no other case with so extensive a series of forms. Indeed, Bourguignat and others have not hesitated to claim a thalassoid aspect for certain Melaniidæ from Nyasa and even from the River Congo (*cf.* **48**, p. 40: **87**, p. 561).

A discussion as to the source from which the striking group of thalassoid Gasteropods has been derived might follow here, but is deferred for consideration at a later stage. It may, however, be pointed out that forms possibly akin to those in Tanganyika which have aroused so much interest, formerly occurred in the Balkan Peninsula (*cf.* Brusina, **58** : **59**), from which neighbourhood distribution through the valley of the Jordan and the Great Rift Valley may have been effected.

Lamellibranchiata.

The Lamellibranchs of the African lakes fall far short of the Gasteropods in point of general interest, since there do not exist in Tanganyika or elsewhere any of those types which have been described as thalassoid. The species belong, in consequence, with but few exceptions, to well-known fresh-water genera such as *Corbicula*, *Unio*, and *Mutela*. The list of species admitted reaches a much smaller total (53) than in the case of the Gasteropoda, and it is quite surprising to find that in this instance Tanganyika does not take the first place with the largest number of different forms. This position is held by Victoria Nyanza with 18 species, but Tanganyika follows very closely with 17, and maintains its reputation to some extent by exhibiting the highest number of endemic species and even certain endemic genera. In the following table no column is provided for Kivu, since there is only a doubtful record of Lamellibranchs from that lake *.

Table of Distribution of Lamellibranchiata †.

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Other parts of the world.
Family Cyrenidæ.						
Corbicula astartina	...	...	P	...	...	Zambezi.
,, cunningtoni......	...	E				
,, radiata	P	P	P	P	P	E. Africa, Nile.
Family Sphæriidæ.						
Sphærium nyanzæ	...	P	...	P	P	E. Africa.
,, stuhlmanni......	...	E				
,, victoriæ	...	E				
Eupera parasitica	...	P	...	...	...	Nile, Abyssinia.
Family Unionidæ.						
Unio acuminatus	...	...	...	E		
,, ægyptiacus	...	...	...	P	...	Nile.
,, bakeri	...	...	...	E		
,, böhmi	E					
,, borellii	...	...	E			
,, burtoni	E					
,, cailliaudi	...	...	...	P	...	Nile.
,, calathus	E					
,, emini	...	E				
,, gerrardi	E					
,, grandidieri	...	E				
,, hauttecœuri	...	E				
,, horei	E					
,, hypsiprymnus	...	...	E			
,, kirki	...	...	P	...	...	Nyasaland.
,, lechaptoisi	...	...	E			
,, liederi	...	...	P	...	...	E. Africa.
,, lourdeli	...	E				
,, monceti	...	E				
,, mossambicensis	...	...	P	...	...	Zambezi, E. Africa.
,, multicolor	...	E				
,, ngesianus	...	...	...	...	E	
,, nyassaënsis	...	...	P	...	...	Angoni Land.
,, rostralis	E					
,, ruellani	...	E				
,, stuhlmanni	...	...	...	...	E	

---

* Speaking of the fauna of Kivu, Moore refers to "one or two species of fresh-water bivalves, closely allied to the Unios found generally in the African lakes" (**137**, p. 129). Against this assertion is to be set the statement of the naturalist at the head of the German Central Africa Expedition, "Ebenso scheinen lebende Lamellibranchier zu fehlen" (**156**, p. xiv).

† The principal sources which may be consulted for information on the Lamellibranchs are Smith (**170**) and von Martens (**116**).

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Other parts of the world.
Unio tanganyicensis	E					
„ teretiusculus	...	...	...	P	...	R. Nile.
„ thomsoni	E					
Burtonia bourguignati	Gen. E					
„ tanganyicensis ...	E					
Brazzæa anceyi	Gen. E					
Family Mutelidæ.						
Mutela alata	...	..	E			
„ bourguignati	...	P	...	..	...	E. Africa.
„ exotica	P	...	...	...	...	N. Africa.
„ nilotica	...	...	...	P	P	Egypt.
„ soleniformis	E					
„ subdiaphana	...	E				
Pleiodon spekei	E					
Spatha anceyi	...	...	E			
„ bloyeti	...	P	...	...	...	E. Africa.
„ kirki	...	...	E			
„ nyassaënsis	...	...	E			
„ trapezia	...	E				
Moncetia anceyi	Gen. E					
Family Ætheriidæ.						
Ætheria elliptica	P	P	...	...	...	Tropical Africa.
5 families	4	5	3	4	4	
11 genera	3 E, 5 P. (8)	7 P.	4 P.	4 P.	4 P.	
53 species	14E,3P. (17)	12E,6P. (18)	7E,6P. (13)	2E,6P. (8)	2E,3P. (5)	

The table of distribution in this case displays no outstanding features such as are to be seen in other groups. The not inconsiderable total of 53 species is reached, but the details of distribution have, in most cases, little significance. Firstly, it may be noted that the vast majority of the forms (there are only 4 exceptions) are on record merely from a single lake; secondly, it is interesting to find that no species in the whole list occurs outside the African continent.

Victoria Nyanza, as already stated, exhibits the largest number of types, viz. 18, but is closely followed by Tanganyika with 17 and by Nyassa with 13. Lakes Albert and Edward follow in the usual order with 8 and 5 species respectively. A fact which emerges from an examination of these figures, is that the two lakes with the highest totals only contain about one-third of the number of species enumerated (Lake Victoria 33·9 per cent., Tanganyika 32 per cent.). Contrasted with this, the Gasteropoda of Tanganyika constitute over 63 per cent. of the total number of Gasteropods enumerated, while in other groups the corresponding figures for Tanganyika reach 80 per cent. and even 90 per cent. (Branchiura).

Tanganyika with 14 endemics out of 17 leads the way as far as endemic Lamellibranchs are concerned (82 per cent.), Lake Victoria coming near with 12 out of 18 (66 per cent.), while Nyasa has 7 out of 13 (54 per cent.). Even the smaller lakes have each two endemic species. It will be observed that the proportion of peculiar forms is very high in this group also; indeed, in some instances it is higher than in the case of the Gasteropods. Endemic genera are known only from Tanganyika, three being retained in the list out of a larger number distinguished by Bourguignat. The genus *Moncetia* of Bourguignat, inserted in the table as endemic, though not definitely rejected, is nevertheless considered by Smith as only doubtfully separable from *Spatha* (**170**, p. 101).

A brief survey of the list of species will suffice. *Corbicula radiata*, a representative of the Cyrenidæ, is the only form which is on record from all the lakes concerned. It is a widely distributed African type, being known from other parts of East Africa and from the valley of the Nile.—The family Sphæriidæ is represented by the genera *Sphærium* and *Eupera*. It is somewhat strange that the four species enumerated are all found in Lake Victoria, but not in Tanganyika or Nyasa. *Sphærium nyanzæ* is known from Victoria, Albert and Edward Nyanzas, as well as from other parts of the continent, but it is associated in Victoria with two additional species which are peculiar to that lake. *Eupera parasitica*, which is a Nilotic and N. African form, is at present only recorded from Victoria Nyanza.—In the family Unionidæ there are associated with the extensive genus *Unio* itself only the two closely related genera *Burtonia* and *Brazzæa*, which are confined to Tanganyika. No fewer than 29 different species of *Unio* are enumerated, not one of which is on record from more than a single lake. Tanganyika exhibits 8 and Lake Victoria 7 endemic species. Of 7 types in Nyasa 3 are endemic; of 5 in Lake Albert 2 are endemic. Lake Edward, lastly, contains 2 forms, both of which are endemic.—In addition to three genera of wider distribution, the Mutelidæ contains the doubtful genus *Moncetia*, to which reference has already been made—a genus described as peculiar to Tanganyika. *Mutela nilotica* is the only species in the family recorded from more than one lake, it being found in both Albert and Edward Nyanza as well as in Egypt. Each of the bigger lakes exhibits a single endemic form of *Mutela*. The genus *Pleiodon* is only represented by *P. spekei*, confined to Tanganyika—it is one of the species named by Woodward from Speke's original collection. *Spatha* is unrepresented in Tanganyika and the smaller lakes, but a series of three endemic forms is known in Nyasa.—Lastly, *Ætheria elliptica*, sole representative of the Ætheriidæ, occurs in Tanganyika and Victoria Nyanza, but has not been recorded from the other lakes, although it is widely distributed in Tropical Africa.

While a considerably smaller number of forms is involved here than was the case with the Gasteropods, there is yet an indication that fewer species occur in the smaller than in the larger lakes. With the exception of Tanganyika, the lakes are arranged in order of size, and the figures for the species are as follows:—Tanganyika 17, Victoria 18, Nyasa 13, Albert 8, and Edward 5. Regarding Tanganyika as a lake apart, the remaining figures fit in satisfactorily with this suggestion.

The features which are characteristic of the different lakes may be summed up in a few words. Tanganyika alone contains endemic Lamellibranch genera. *Sphærium*, *Eupera*, and *Spatha* are unrepresented, but a number of endemic species of *Unio* are known.—Victoria Nyanza, with the largest total of species, displays, notwithstanding, little of interest. Most of the genera are represented, except those peculiar to Tanganyika, and a series of forms belonging to *Sphærium* and *Unio* are to be observed.—Of Nyasa there is likewise little to record. The lake only contains species from the four well-known genera *Corbicula*, *Unio*, *Mutela*, and *Spatha*, 3 endemic types of the last-mentioned being an outstanding feature.—Both Albert and Edward Nyanza are similar in type to Nyasa, but contain a representative of *Sphærium* and not *Spatha*.

From this survey of the Lamellibranchs, the following points emerge:—No thalassoid types occur in Tanganyika, but that lake contains a number of endemic species, as well as three endemic genera. All the lakes show a high percentage of endemic forms, but in most cases these are merely species belonging to widely distributed genera. While Tanganyika does not exhibit in this instance so remarkable a series of unique genera and species as in the case of the Gasteropods and other groups, it retains nevertheless a distinctness from the remaining lakes quite in keeping with its general character.

MACRURA.

The only Macrurous Crustacea which appear to occur in the big African lakes are the prawns, these being quite common types in the fresh-waters of the tropics. An examination of the forms now known to exist in the lakes of Africa reveals, however, many points of interest. In the first place, no fewer than twelve species have been discovered in Tanganyika, of which ten were obtained for the first time by the Third Tanganyika Expedition. This is in itself a large number of different species to be found within the limits of a single lake, but the interest is greatly increased when it is realised that all these forms occur in Tanganyika alone. This is the only well represented group in which such is the case. Again, with the exception of a single species of the well-known fresh-water genus *Palæmon*, all the genera are equally to be regarded as endemic.

Table of Distribution of Macrura [†].

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert[*] Nyanza.	Edward Nyanza.	Other parts of the world.
Family PALÆMONIDÆ.						
Palæmon moorei	E					
Family ATYIDÆ.						
Caridina nilotica var. gracilipes	...	P	P	P[*]	P	Asia, Australia.
Limnocaridina retiarius	Gen. E					
" parvula	E					
" tanganyikæ ...	E					
" similis	E					
" latipes	E					
" socius	E					
" spinipes	E					
Limnocaridella alberti	...	...	...	Gen. E		
Caridella cunningtoni	Gen. E					
" minuta	E					
Atyella brevirostris	Gen. E					
" longirostris	E					
6 genera	3E, 1P.	1 P.	1 P.	1E, 1P.	1 P.	
14 species	12 E.	1 P.	1 P.	1E, 1P.	1 P.	

The adjoining table shows at a glance the most striking feature of distribution, namely that while *Caridina nilotica* var. *gracilipes* [‡] occurs in nearly all the big lakes of Africa, it is not found in Tanganyika, but is replaced there by 12 endemic species belonging for the most part to endemic genera. Lake Albert also contains an interesting endemic form (obtained by the German Central Africa Expedition and described by Lenz (**109**, p. 132) and Bouvier (**52**, p. 575)) in addition to the above-mentioned widely distributed *Caridina*, while Kivu is the only lake of those at present under review in which prawns have not hitherto been observed.

The first species of prawn ever taken in the African lakes was obtained in Victoria Nyanza by Stuhlmann in 1890 (**100**, p. 36). It was re-taken in the lake by Neumann, and more recently by Alluaud, by myself, and by Degen. From Nyasa a species of prawn was brought for the first time by my expedition. These species prove to be one and the same form—the *Caridina nilotica* var. *gracilipes*, to which reference has just been made. During the German Central Africa Expedition of 1907–08 this prawn was collected by Schubotz in both Lakes Albert * and Edward (**109**, p. 130). It is thus the only common species in the African lakes, while it has in fact a yet wider distribution, ranging in Africa from Natal to the Nile and extending into Asia and Australia. The eastward range of this type has indeed an additional interest on account of the well-marked resemblance noticeable in other groups between the East African and Indian faunas.

[†] A detailed account of the Macrura of the Third Tanganyika Expedition is given by Calman (**61**), and forms the principal source of information on this group.

[*] The species of prawn collected by Schubotz at Kassenje on Lake Albert was described by Lenz (**109**, p. 130) as *Caridina longirostris* Milne-Edwards. It is, however, commonly agreed that *longirostris* is identical with the earlier *nilotica*, so that, apart from the varietal name, this is the same form that occurs so widely distributed in Africa. Since the type described as *Caridina nilotica* var. *gracilipes* is certainly rather variable, it seems probable that the Lake Albert specimens are not sufficiently distinct to be recorded under a different name, and this is the view which I have taken in compiling the table of distribution above. For a discussion of these questions of synonymy consult the paper of Calman (**61**, p. 189 *et seq.*) and the subsequent paper of de Man (**110**), which arrives at somewhat different conclusions.

[‡] I adopt the varietal identifications of Hilgendorf (**100**), Calman (**61**), and Lenz (**109**), but it is only right to point out that de Man (**110**) takes a different view. He appears to consider that the form occurring in Lake Victoria is to be referred to the typical *Caridina nilotica* itself, and the form from Nyasa to his newly established variety *natalensis*. The type *Caridina nilotica* var. *gracilipes* he records only from the islands of Celebes and Salayer in the Malay Archipelago.

Only the first of the twelve species enumerated from Tanganyika can be compared at all closely with forms which are known from other parts of the world, and it has no very pronounced affinities. The remaining eleven species belong to the group of the Atyidæ, and are not so nearly connected with types hitherto known. Moreover, in common with *Limnocaridella alberti*, they differ from all the other species of the family in having a smaller number of branchiæ †, which is a feature undoubtedly due to specialisation.

To sum up then, there occurs in most of the great lakes of Africa only a single species of prawn having a very wide distribution. In Lake Albert this is associated with an endemic form, and in Tanganyika it is replaced by twelve other endemic forms, the majority of which are among the most highly specialised members of the family to which they belong. Under the circumstances, it is impossible to resist the suggestion that there is exhibited here something very similar to what was seen in the case of the fishes, and particularly the Cichlidæ. If the extraordinary variety of form, and high degree of specialisation, which is characteristic of the Cichlids of Tanganyika, may have been due to prolonged isolation and comparative freedom from competition, it at least seems not improbable that the remarkable Macruran fauna of the lake owes its origin to the same cause ‡.

BRACHYURA.

There are five different species of crabs now known from Tanganyika, of which one has been left unnamed for the present. In a manner closely corresponding with the case of the prawns,

---

[*] See footnote above.

[†] A reduced branchial formula is also characteristic of the remarkable West Indian form for which Bouvier has established the genus *Micratya* (**51**, p. 181), formerly *Calmania* (**50**, p. 334). Bouvier regards this as allied to the Tanganyikan genera, but this view is not accepted by Calman (**62**, p. 796).

[‡] An important paper dealing with the origin of the peculiar prawn fauna of Tanganyika was communicated by Bouvier to the International Zoological Congress at Monaco (**52**). Consult also Bouvier's paper on the classification of the Atyidæ (**51**).

while two species belong to a widely distributed and common fresh-water genus (*Potamonautes*), the remaining three, though members of the typical fresh-water group (Potamonidæ), constitute a remarkable genus, which occurs only in Tanganyika. All the forms from the other lakes under review belong to well-known genera of the same family. No Brachyurans have as yet been reported from Albert Nyanza.

Table of Distribution of Brachyura †.

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Edward Nyanza.	Kivu.	Other parts of the world.
Family Potamonidæ.						
Potamon (Potamonautes)						
inflatus ...	...	...	P	...	...	Natal.
„ „ orbitospinus	...	...	E			
„ „ platynotus..	E					
„ „ sp.?	...	...	P			
„ „ sp.?	P					
Potamon (Geothelphusa)						
berardi ...	...	...	...	...	P	Egypt, Abyssinia.
„ „ emini	...	P	...	P	P	E. Africa, Abyssinia.
Potamon (Acanthothelphusa)						
niloticus	...	P	...	...	...	Egypt, Abyssinia.
Platythelphusa armata........	Gen. E					
„ maculata ...	E					
„ conculcata ...	E					
4 genera and subgenera...	1 E, 1 P.	2 P.	1 P.	1 P.	1 P.	
11 species	4 E, 1 P.	2 P.	1 E, 2 P.	1 P.	2 P.	

The table of distribution makes it clear that while each of the lakes in the list exhibits one or more representatives of the very well-known genus *Potamon* with its sub-genera, these types are associated in Tanganyika with three species of an interesting endemic genus. Both Nyasa and Tanganyika possess species of *Potamonautes* which are peculiar to themselves, but it is in Tanganyika alone among the big lakes that an endemic genus is found. All the species enumerated appear to be confined to the continent of Africa.

Apart from the case of Tanganyika, it will be noted that (with the exception of *Potamon* (*Potamonautes*) *orbitospinus* from Nyasa), the forms from the different lakes are by no means confined to them, and indeed are often of wide distribution. This whole series of types—types such as are known from all the tropical fresh-waters of the Old World—may be considered as the normal African group, and calls for little further remark. In the paper already cited (**70**, p. 263) the present writer expressed a conviction that the number of African species has been unduly multiplied, and the unnamed forms included in the table are to be regarded as specimens which, in the existing state of our knowledge, it is impossible to identify. It is nevertheless clear that the precise distribution in the lakes of these representatives of the subgenera of *Potamon* is of little, if any, significance.

---

† For further details concerning most of these forms, consult the Report on the Brachyurous Crustacea of the Third Tanganyika Expedition (**70**).

In this connection it should perhaps be explained that the grounds of identification of the river-crabs are unsatisfactory on the whole, external characters of a comparatively trivial and fluctuating nature forming the basis of distinction. Systematists are thus on less sure ground than in the case, for instance, of the prawns, where a matter like the branchial formula affords more satisfactory evidence of affinity.

Tanganyika, with no less than three species of the endemic genus *Platythelphusa*, is evidently a case *sui generis*. There are certain features in the anatomy of this unique genus which suggest that it is of a somewhat primitive and unmodified character, but at the same time nothing to indicate that it is more definitely marine than the other members of the family to which it belongs. Further, it is only to be regarded as unspecialised in comparison with allied forms which have adopted a semi-terrestrial mode of life, so that it affords in reality no support for Moore's view that Tanganyika is the altered remains of an ancient sea. The genus with its three distinct species is rather to be looked upon as one more example of variation and divergence, brought about, in all probability, by prolonged isolation. Finally, it may be noted that this lake, with five species, contains a larger number of different crabs than any of the others under consideration.

Those groups of smaller Crustacea which are often associated under the heading Entomostraca, are (with the exception of the marine Cirripedia) well represented in the African lakes. Information concerning them is, however, for the most part, of fairly recent date, since such organisms would be overlooked by any but trained biologists, and the use of the tow-net in Central Africa has even yet yielded results which are but fragmentary and incomplete. All the earlier records are due to the zeal and energy of Stuhlmann, and concern in particular Lakes Victoria and Edward. In 1898–1900, extensive collections were made in Nyasa and its neighbourhood by Fülleborn, and this material, together with a supply from Victoria Nyanza collected by Borgert, forms the basis of a comprehensive treatise by Daday (76), in which the whole of the microfauna is dealt with. The collections made by the writer during the Third Tanganyika Expedition have afforded information for the first time concerning the Entomostraca of Tanganyika, as well as providing additional records for Nyasa and Lake Victoria. Finally, the work of Schubotz during the German Central Africa Expedition has furnished further particulars relating to Lakes Kivu, Edward, and Albert.

It may here be pointed out that these lower Crustacea, with the exceptional opportunities they are known to possess for obtaining world-wide distribution, cannot afford evidence of the same value as the higher forms. When—as is particularly the case among the Cladocera—even specific forms of cosmopolitan range reappear in the great lakes, it becomes clear that the precise geographical distribution of such species is a matter of no great significance. At the same time, the possibility is not excluded that the lakes may differ in their suitability to harbour certain types, while it is highly probable that new types can and will develope in some cases, constituting species or even genera of an endemic nature. Thus a study of the distribution of these forms in the lakes of Central Africa is nevertheless not devoid of interest, and may indeed furnish testimony of some importance.

EUCOPEPODA.

The Eucopepoda so far observed in the lakes with which this paper is concerned reach the not inconsiderable total of 54 species. Of these, more than half (31) have been found in Tanganyika, to which lake a large proportion exclusively belong. There is every reason to believe that further investigation will bring to light additional forms, particularly from Victoria Nyanza and the smaller lakes, which, in this respect, have received less attention than Tanganyika and Nyasa.

Table of Distribution of Eucopepoda †.

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Kivu.	Other parts of the world.
Family CENTROPAGIDÆ.							
Diaptomus galeboides ‡	...	P	...	P			
„ mixtus	...	...	E				
„ africanus	...	...	P	...	...	...	E. Africa.
„ stuhlmanni	...	E					
„ simplex	E						
„ cunningtoni	...	...	E				
„ kraepelini	...	...	P	..	...	...	E. Africa.
Family HARPACTICIDÆ.							
Canthocamptus schröderi	...	E					
Attheyella decorata	...	...	P §	...	...	...	Asia, S. America.
„ grandidieri	...	...	P §	...	...	...	S. America, New Guinea.
Dactylopus jugurtha	...	...	P	...	...	...	Asia, New Guinea.
Schizopera inopinata	E						
„ validior	E						
„ consimilis	P	P					
„ ungulata	E						
„ minuticornis	E						

---

† Detailed information concerning a large proportion of these species is given by Sars (**151**). The other sources of most importance are Daday (**76**, p. 106) and Mrázek (**139**). For the Lernæidæ consult Cunnington (**73**).

‡ I follow Sars (**151**, p. 34) in assuming that this form, which is one of the commonest and most characteristic species of Lake Victoria, is not identical with the Egyptian *D. galebi* Barrois, as supposed by Mrázek and Daday.

§ Not actually recorded from the lake itself, but from within its drainage area.

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Kivu.	Other parts of the world.
Schizopera spinulosa ……	E						
„ fimbriata …..	…	…	E				
„ scalaris ………	E						
Ilyophilus perplexus………	E						
Family Cyclopidæ.							
Cyclops aspericornis ………	…	…	P §	…	…	…	East Indies.
„ leuckarti ………..	P	P	P	P	P	P	Cosmopolitan.
„ emini …………..	…	P	P	..	…	..	E. Africa.
„ neglectus* ………	P	P	P	P	P	P	Senegal, Sumatra.
„ tenellus ………..	E						
„ albidus …………..	…	…	P	…	…	…	Cosmopolitan.
„ attenuatus ………	E						
„ varicans ………..	P	…	P	P	..	…	Europe, New Zealand.
„ bicolor …………..	…	…	P §	…	…	…	E. Africa, Europe.
„ exiguus ………..	E						
„ cunningtoni ……	E						
„ pachycomus ……	E						
„ serrulatus † ……	…	P §	P §	..	P	…	Cosmopolitan.
„ semiserratus ……	E						
„ lævimargo ………	E						
„ macrurus ………..	…	…	P	…	…	…	Cosmopolitan.
„ angustus ………..	P	…	P	P			
„ stuhlmanni ………	…	E					
„ rarispinus ………	E						
„ agiloides ………..	P	P	…	P			
„ euacanthus ………	E §						
„ ciliatus ………..	E						
„ dubius …………..	…	…	E				
„ prasinus ………..	…	P	P	…	..	…	E. Africa, Europe.
„ phaleratus ………	…	P §	P §	…	…	…	Cosmopolitan.
„ compactus ………	P §	…	…	…	..	…	Central Africa.
„ oligarthrus ………	E						
Family Ergasilidæ.							
Ergasilus kandti ………..	…	…	…	E			
„ sp. ………………	…	P	P				
Ergasiloides megacheir …	E						
„ macrodactylus	E						
„ brevimanus …	P	…	P				
Family Lernæidæ.							
Lernæocera diceracephala ..	E						
„ haplocephala …	P	…	…	…	…	…	Nile, Congo.
10 genera ………………	6 P.	5 P.	7 P.	3 P.	1 P.	1 P.	
54 species ………………	22E,9P. (31)	3E,10P. (13)	4E,19P. (23)	1E,6P. (7)	3 P.	2 P.	

---

§ Not actually recorded from the lake itself, but from within its drainage area.

* As explained by Sars (**151**, p. 51 & **74**, p. 82), this species has been wrongly identified with *C. oithonoides* G. O. Sars or with *C. hyalinus* Rehberg by other writers on African Copepoda. I adopt the new name introduced by Sars.

† A number of the forms which succeed this in the list belong to the group for which *C. serrulatus* Fischer is the type. While the species *C. serrulatus* is recorded by Mrázek (**139**, p. 3) for Victoria Nyanza, by Daday (**76**, p. 108) for Nyasa, and by van Douwe (**80**, p. 492) for Edward Nyanza, it is not unlikely that the specimens in question might rather belong to one of the species in the "*serrulatus*" group as described from the lakes by Sars, than to *C. serrulatus*, s. str. At present it is impossible to settle this point, so I take the course least open to objection and insert the records of Mrázek, Daday, and van Douwe as they stand.

An examination of this long list of forms reveals in the first place the large proportion of the recorded species which has been observed in Tanganyika. The latter lake contains 31 out of a total of 54 different forms, Nyasa contains 23, Victoria Nyanza 13, and the remaining lakes still smaller numbers. The contrast between the lakes is greater than is disclosed by these figures, for out of 31 species known from Tanganyika, 22 are peculiar to that lake, and in comparison only 4 out of 23 for Nyasa and 3 out of 13, for Lake Victoria. In the three smaller lakes there is only a single recorded species which is endemic, and that occurs in Albert Nyanza. Expressed in percentage form, this means that nearly 71 per cent. of the Copepods of Tanganyika are found in that lake alone, while of the species found in Nyasa only some 17 per cent. are peculiar to the lake, in Victoria 23 per cent., and in Albert 14 per cent. Excluding Tanganyika, it will be observed that only 8 of the forms recorded are endemic, so that with 22 endemic species, Tanganyika has nearly three times as many endemic Eucopepoda as the other lakes can muster between them.

Turning now to the distribution of families and genera in the lakes, the genus *Diaptomus*, sole representative of the Centropagidæ, calls for little comment. A single species of this genus occurs in Tanganyika, to which it is peculiar: it appears to be a most characteristic plankton form in that lake. Lakes Victoria and Nyasa each contain endemic species as well as types of wider distribution, so that the three big lakes may each be said to have their own particular forms. None of the species of *Diaptomus* in this list have been observed outside the continent of Africa.

The representatives of the Harpacticidæ are of far greater interest. An endemic species of *Canthocamptus* has been recorded from Victoria Nyanza, and widely distributed species of *Attheyella* and *Dactylopus* from Nyasa. It is on the genera *Schizopera* and *Hyophilus*, at one time regarded by Sars as strictly marine, that interest really centres. The genus *Schizopera* is represented in the collections made by the writer by no less than 8 species, of which 6 are peculiar to Tanganyika and one to Nyasa, while one occurs in both Lakes Tanganyika and Victoria. The genus was established by Sars for the reception of a species found in a brackish-water lagoon on the Chatham Islands, while subsequently species have been obtained from the Caspian and from Egypt. It is obvious that such a genus can hardly be regarded as strictly marine. Three questions suggest themselves in this connection. How does the genus come to be represented in the heart of Africa; how is it that brackish-water types are living there in perfectly fresh-water; and how is it that so many different species are recognisable in Tanganyika? Sars points out (**151**, p. 69) that the most obvious explanation would be to regard these as genuine "relict" forms, in which case the Tanganyikan species would be important members of Moore's so-called "halolimnic" series. He rejects on general grounds the view advanced by Moore, and indicates transport by the aid of migratory aquatic birds as sufficient explanation for this remarkable discontinuous distribution. He asserts the probability that forms transported from brackish water would not be unable to survive in fresh water, and finally maintains that the several species occurring in Tanganyika have been produced by divergence during a period of isolation—a view entirely in accord with that already expressed in the case of other animal groups.—The genus *Ilyophilus* is represented in Tanganyika by a single species which is endemic. The type species of this genus was described from the Baltic and has also been obtained near Christiania, so that the remarks concerning transport and establishment in fresh water are as applicable here as in the case of *Schizopera*.

No fewer than 27 species, all belonging to the genus *Cyclops*, are enumerated under the family Cyclopidæ. It will be noted that Tanganyika again leads the way with 17 species, while Nyasa contains 13 and Lake Victoria 8: moreover, 11 of the Tanganyikan species are peculiar to that lake, while the other two lakes each contain only a single endemic form. The three smaller lakes possess fewer representatives, viz.:—Lake Albert 5, Lake Edward 3, and Lake Kivu only 2. All the latter are of fairly wide—some of cosmopolitan—distribution.

The family Ergasilidæ, which may be regarded as intermediate between the free-living and the highly degenerate parasitic Copepods, is represented by 5 species belonging to two genera. An endemic form of the genus *Ergasilus* has been recorded from Albert Nyanza, and the genus has also been recognised both in Nyasa and Victoria. In Tanganyika it would seem to be replaced by the genus *Ergasiloides*, described from material obtained by my expedition. Two endemic species are on record from Tanganyika, while a third is found in that lake and also in Nyasa.

The Lernæidæ with two forms of *Lernæocera* concludes the list. The two species were obtained by the Third Tanganyika Expedition from fishes in that lake, and while one proves to be endemic, the second was found to be identical with specimens in the British Museum collection taken on Nile fish.

Reference may again be made here to the statement that the number of different animal forms existing in the lakes varies in proportion to the size of the latter (*cf.* pp. 535, 548). It is only when many forms are enumerated that such a comparison is justified, but in this case it may fairly be undertaken. Apart from Tanganyika, the lakes are arranged in the table in descending order as regards size, and the total figures are as follows:—Tanganyika 31 (species), Victoria 13, Nyasa 23, Albert 7, Edward 3, and Kivu 2. It is very clear that Tanganyika is quite unique, but apart from that lake, beginning with Victoria Nyanza, the Copepods exhibit a regularly decreasing total with the exception of Nyasa, where the higher figure is probably due to the more thorough exploration of its waters.

The distribution of Copepoda in the individual lakes may be summarised as follows:—Tanganyika, with 31 species, 22 of which are endemic, is clearly in a category by itself. Containing a single species of *Diaptomus* which is peculiar to it, the lake is chiefly characterised by a number of remarkable forms belonging to the genera *Schizopera* and *Hyophilus*, nearly the whole of which are not known elsewhere. Even of the cosmopolitan genus *Cyclops*, Tanganyika exhibits 11 endemic types, as well as others of wider distribution, while of the three species of *Ergasiloides*, two are found here alone. Two forms of the parasitic *Lernaeocera* occur in the lake, one of which is likewise endemic.

The Copepoda of Lake Victoria are referred not only to fewer types, but form a much less interesting assembly. They comprise a single endemic species in each of the genera *Diaptomus*, *Canthocamptus*, and *Cyclops*, but otherwise are forms of wider, often of world-wide distribution.

A larger number of species is known from Nyasa, but out of 23, only 4 are endemic. Of the latter, two are species of *Diaptomus*, while there is a single endemic form of the striking genus *Schizopera* and one of *Cyclops*. Most of the remaining species are widely distributed, a considerable proportion being well-known forms of *Cyclops*. Nyasa contains a species of *Ergasilus* as well as *Ergasiloides brevimanus* which is otherwise confined to Tanganyika. There is no reason to suppose that Nyasa will be found to contain so many more Copepoda than Victoria Nyanza when the latter lake has been equally well investigated.

Seven species have been observed in Lake Albert, of which merely a single form (*Ergasilus kandti*) is endemic. Apart from this and from a species of *Diaptomus* found also in Lake Victoria, the lake contains only representatives of the genus *Cyclops*, which are of fairly extended, and in some cases of the widest possible range.

Lake Edward with 3 species, and Kivu with 2, come last in the series, and it should be noted that not only do they contain very few types of Copepoda, but that these types have little significance, being in each case widely distributed species of *Cyclops*.

It is thus apparent that with increase in size the lakes exhibit an increase in the number of forms which they contain; that only in the larger lakes do endemic species appear; and, finally, that Tanganyika possesses a large number of unique types which may well have been produced during a period of prolonged isolation.

BRANCHIURA.

This small group of animals, which are parasitic for the most part on fish, was for long but poorly represented in the collections from the great lakes of Africa. The collections made by Stuhlmann in Victoria Nyanza (**184**, p. 154) and Edward Nyanza (**187**, p. 47 & **188**, p. 37) and by Fülleborn in Nyasa (**187**, p. 47 & **188**, pp. 37 & 44), resulted in a total of three species belonging to as many genera. To these may now be added no fewer than seven new species of *Argulus* which were obtained for the first time by the Third Tanganyika Expendition (**72**), while there are further records of distribution now available which make our knowledge more complete. It is safe to predict that future investigation will add to the localities in Africa from which these parasitic forms are known, even though it may not materially increase the number of recognised species.

Table of Distribution of Branchiura †.

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Other parts of the world.
Dolops ranarum	P	P	P	...	...	Nile.
Argulus incisus	E					
„ rubropunctatus ...	E					
„ personatus	E					
„ exiguus	E					
„ angusticeps	E					
„ striatus	E					
„ rubescens	E					
„ africanus	P	P	P	P	P	Nile.
Chonopeltis inermis	...	...	Gen. E			
10 species	7 E. 2 P.	2 P.	1 E, 2 P.	1 P.	1 P.	

The outstanding feature revealed in the above list is that while two species occur widely distributed in Africa, these are associated in Nyasa with a single endemic form, but in Tanganyika with no less than seven. Thus out of ten known African species, nine are found in Tanganyika, which is therefore seen to possess not only a larger number of characteristic species, but a much richer Branchiuran fauna than the other great lakes with which it may reasonably be compared. All the species enumerated are confined to the African continent so far as is at present known. *Dolops ranarum* is the only African representative of a genus which is otherwise exclusively American. The genus *Chonopeltis* was established from a single female specimen from Lake Nyasa, while *Argulus* alone has a distribution which is world-wide.

OSTRACODA.

It seems probable that the Ostracod-fauna of the great lakes is less well represented in the collections hitherto obtained than is the case with any of the other groups of Entomostraca. This is due to the fact that nearly all fresh-water Ostracods are bottom-living rather than planktonic forms, and require other methods than surface tow-netting for their capture, while the bulk of the material at present examined was collected by the tow-net. This implies, of course, that many additional types will probably be found when the lakes are more adequately explored. Nevertheless, 22 species are on record for Tanganyika (of which 20 are peculiar to that lake), and 17 and 7 respectively for Nyasa and Victoria Nyanza. No Ostracoda have so far been recorded from Lakes Edward and Kivu.

---

† For further particulars, bibliography, etc., consult Cunnington (**72**).

Table of Distribution of Ostracoda †.

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Other parts of the world.
Family CYPRIDÆ.					
Cypria castanea	...	...	P	...	Natal.
,, lenticularis	...	...	P §	...	Madagascar.
Paracypria declivis	E				
,, complanata	E				
,, conoidea	E				
,, obtusa	P	...	...	P	
,, deflexa	E				
,, subangulata	E				
,, reniformis	E				
,, humilis	E				
,, opaca	E				
,, claviformis	E				
,, flexuosa	E				
,, curta	E				
Iliocypris propinqua	...	...	E		
,, alta	E				
Heterocypris dubia	...	E			
Eucypris flabella	...	E			
,, inermis	...	...	P §	...	Natal.
,, laticauda	...	...	E §		
Stenocypris sinuata	...	...	P §	...	Madagascar.
,, malcolmsoni	...	P	...	...	Asia, Australia.
,, marginata	...	...	E §		
,, perarmata	P	...	P	...	Natal.
,, fülleborni	...	...	E §		
,, fasciculata	...	...	E §		
,, stagnalis	...	...	E		
Cypridella fossulata	...	...	P §	...	Kilimandjaro.
Cypridopsis obliquata	E				
,, sinuata	E				
,, cunningtoni	...	...	E		
,, pusilla	E				
,, monodonta	E				
,, serrata	E				
,, bidentata	E				
,, tumidula	E				
,, congenera	E				
,, gibba	...	E			
Potamocypris fülleborni	...	...	E		
,, viduella	...	...	P §	...	Cape Colony.
Zonocypris costata	...	P	P §	...	E. Africa, Madagascar.
,, lævis	...	E			
Family CYTHERIDÆ.					
Limnicythere obtusata	...	E			
,, michaelseni	...	...	P §	...	Lake Rukwa.
11 genera	4 P.	6 P.	9 P.	1 P.	
44 species	20 E, 2 P. (22)	5 E, 2 P. (7)	8 E, 9 P. (17)	1 P.	

---

† This account is based in the main on the report published by Sars on the Ostracoda collected by the Third Tanganyika Expedition (**152**).

§ Not actually recorded from the lake itself, but from within its drainage area.

The existence of a large number of Ostracods which are peculiar to Tanganyika is the principal feature displayed by the list of species. Of the total number of forms on record, it will be noted that Nyasa with 17 species does not fall far short of Tanganyika with 22, while Victoria Nyanza is a long way behind with only 7. This is probably due—at all events in part—to the fact that Nyasa and its drainage area have been more thoroughly investigated in this direction than Lake Victoria. It may further be remarked that less than half the records from Nyasa are from the actual waters of the lake itself, the remainder coming from ponds and swamps etc. in the vicinity. Corresponding collections from the surrounding ponds, swamps, and rivers are wanting in the case of both Victoria and Tanganyika; indeed, the whole of the material collected in the three biggest lakes by the author's expedition came only from the lakes themselves. Additional records are therefore to be expected, particularly from Lakes Victoria and Tanganyika whenever a more complete investigation of the Entomostraca becomes possible.

While Nyasa is shown to contain nearly as many different forms as Tanganyika, it will be seen that in the nature of these forms the lakes differ profoundly. More than half the species from Nyasa have also been obtained elsewhere, but of the 22 species from Tanganyika only two have so far been observed outside the confines of that lake, or to put it in another manner, 47 per cent. of the Nyasa forms are endemic in the lake, while nearly 91 per cent. are endemic in the case of Tanganyika.

Another feature of distribution which this table brings into prominence is the association of certain groups of forms with certain lakes. Only in three cases have species been recorded from more than one lake—*Stenocypris perarmata* from Tanganyika and Nyasa, *Zonocypris costata* from Victoria and Nyasa, and *Paracypria obtusa* from Tanganyika and Albert. In every other instance the species from the lakes differ from one another, and appear to be either peculiar to or at least characteristic of the lakes in which they are found. Without referring to the species seriatim, it may be pointed out that the genera *Stenocypris*, *Potamocypris*, and *Cypria* seem to be associated in particular with Nyasa, and *Cypripodsis* with Tanganyika, while *Paracypria*, with the exception of a single species, occurs only in Tanganyika among the lakes.

Apart from the forms peculiar to Tanganyika (which number 20 out of a total of 44 in the list of Ostracoda), it is to be observed that 8 species are peculiar to Nyasa and 5 to Victoria Nyanza, or 13 in all. It will thus be seen that when Tanganyika is excluded, more endemic forms are known from the remaining lakes than is the case among the Copepoda. It is also singular to note how restricted is the distribution of even the non-endemic forms recorded, for only in a single case (that of *Stenocypris malcolmsoni* which is known from Asia and Australia) has a species been obtained outside the continent of Africa with Madagascar.

To the genera *Paracypria* and *Cypridopsis*, which are so largely represented in Tanganyika, it is necessary to call special attention on account of their remarkable nature. Of the former genus, no fewer than twelve different species have been described from that lake, eleven of which are peculiar to it, and they all, as Sars points out (**152**, p. 756), exhibit striking features of specialisation. It is also a remarkable coincidence—if it is only that—that the type species of *Paracypria* was obtained from the same brackish lagoon on the Chatham Islands as was the type of the Copepod genus *Schizopera*, which is likewise very characteristic of Tanganyika among the lakes. The case of *Cypridopsis* is perhaps more significant still, since of the ten species obtained by the Third Tanganyika Expedition two only display all the features characteristic of the genus, and these are the two forms taken respectively in Lakes Nyasa and Victoria. The other eight types, which are confined to Tanganyika, exhibit certain divergences which suggest that they might more suitably be removed to a new genus which would then be endemic in the lake (**152**, p. 757).

It is quite clear that in the case of this group also, Tanganyika contains an unusually large number of forms, an exceptional proportion of which are peculiar to the lake, and that of these peculiar forms many show undoubted signs of specialisation.

CLADOCERA.

The outstanding fact concerning the Cladocera is the absence of any representatives from the plankton of Tanganyika, and also apparently of Kivu, which is in direct communication with it. Thus the survey of this group of organisms resolves itself into a comparison of the records from the remaining lakes, and this, it is not surprising to find, lacks the interest which the inclusion of species from Tanganyika usually affords.

Table of Distribution of Cladocera †.

Name of Species.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Other parts of the world.
Family SIDIDÆ.					
Parasida szalayi	...	P	...	...	Asia.
Diaphanosoma excisum ...	P	P	...	P	E. Africa, Australia.
Family DAPHNIDÆ.					
Daphnia kirimensis	..	...	...	E	
,, longispina	P	...	...	...	Cosmopolitan.
,, hyalina	P	...	...	...	Cosmopolitan.
,, lumholtzi	P	P	...	...	Palestine, Australia.
,, monacha	...	...	E		
Hyalodaphnia barbata	P	...	...	...	E. Africa.
Ceriodaphnia bicuspidata...	P	...	...	P	
,, cornuta	P	P §	...	...	Asia, Australia, S. America.
,, dubia	P	..	...	...	Sumatra.
,, rigaudi	P	P §	...	P	Almost cosmopolitan.

† For further particulars consult especially Daday (**76**, p. 120). Additional records for Lake Victoria are given by Delachaux (**77**) and for the smaller lakes by Brehm (**54**).

§ Not actually recorded from the lake itself, but from within its drainage area.

Name of Species.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Other parts of the world.
Simocephalus vetulus	P	P	..	...	Cosmopolitan.
Moinodaphnia macleayi ...	...	P §	..	...	Almost cosmopolitan.
Moina dubia	P	P	...	...	E. Africa, Egypt.
„ micrura	P	...	...	...	Zanzibar.
„ sp.	...	...	...	P	
Family BOSMINIDÆ.					
Bosmina longirostris	P	P	...	..	Cosmopolitan.
Bosminopsis deitersi	...	P	...	...	Central Africa, S. America.
Bosminella anisitsi	...	P	...	...	S. America.
Family MACROTHRICIDÆ.					
Macrothrix laticornis	P	P §	...	...	Cosmopolitan.
„ hirsuticornis ...	...	P §	..	...	Algiers, Europe.
„ chevreuxi	P	P	...	...	Africa, S. America.
Ilyocryptus longiremis ...	P	P §	...	..	Cosmopolitan.
Family CHYDORIDÆ.					
Camptocercus australis ...	P	...	..	...	Australia.
Alonopsis singaiensis	...	P	...	...	Ceylon, S. America.
Euryalona orientalis	...	P	...	...	Ceylon, S. America.
Pseudalona longirostris ...	...	P §	...	...	S. America. New Guinea.
Alona affinis	P	...	...	...	Cosmopolitan.
„ costata	P §	...	...	...	Europe.
„ guttata	P §	...	...	...	E. Africa, Europe.
„ pulchella	...	P	...	...	Australia, S. America.
„ quadrangularis	...	P §	...	...	Europe.
„ rectangula	P	P	...	P	Cosmopolitan.
Rhynchotalona rostrata ...	P §	...	...	...	Europe.
Alonella excisa	...	P §	...	...	Europe.
„ globulosa	...	P	...	...	Ceylon, S. America.
„ karua	...	P	...	...	Australia, S. America.
„ punctata	P	...	...	...	E. Africa, S. America.
„ diaphana	P	...	...	...	Australia, S. America.
Pleuroxus similis	...	P §	..	...	S. America.
„ striatus............	...	P §	...	...	Europe, N. America.
„ assimilis	P §	..	..	...	Natal.
Chydorus barroisi	P	...	..	...	Asia, S. America.
„ sphaericus	P	P	...	...	Cosmopolitan.
„ ventricosus	P §	P §	...	...	Ceylon, S. America.
„ leonardi	P	...	...	...	Australia.
„ piger	P §	...	...	...	Europe.
„ globosus	...	P §	..	...	Europe.
Dadaya macrops	...	P §	...	...	Asia, S. America.
Monospilus dispar	P	...	...	..	Europe, N. America.
24 genera	16 P.	20 P.	1 P.	5 P.	
51 species	31 P.	30 P.	1 E.	1 E, 5 P.	

§ Not actually recorded from the lake itself, but from within its drainage area.

The list of Cladocera from the big lakes of Africa differs from all the corresponding lists in the absence of a column for Tanganyika. While the group is entirely unrepresented in Lake Tanganyika itself, various Cladocera occur in the surface tow-nettings which I made in the broad mouth of the Lofu River, which enters the south-western corner of the lake. I had intended myself to report on the Cladocera collected by the Third Tanganyika Expedition, but I have not yet been able to do so, and the specimens from the Lofu remain unexamined. During his investigations on the Copepoda and Ostracoda of the expedition, G. O. Sars, however, kindly isolated and identified certain Cladocera from Victoria Nyanza and Nyasa, and these forms are included in my list of species without further comment, although they constitute in some cases new records of distribution.

The reason for the absence of Cladocera from Tanganyika remains a matter for speculation, but the most likely explanation would seem to be that the water of the lake either contains certain salts which are fatal to such organisms, or is perhaps of too saline a nature to permit them to survive. Colour is lent to this view by the already-mentioned occurrence of Cladocera in the river Lofu and also by the marked difference in nature of the Rotatorian fauna of the lake proper and the river mouth. Rousselet (**150**, p. 794) reports that in a small quantity of material from the river he distinguished 23 different species of Rotifera, while in a large series of tow-nettings from different parts of Tanganyika he was only able to find 10 species, of which but one was common to lake and river. It thus seems highly probable that though the salinity of the lake water has not made it impossible for certain Rotifers to live in Tanganyika, it is at least the factor which has determined the striking difference between lake and river in this respect. Further, it may be pointed out that a somewhat similar state of affairs has been observed in the case of the phytoplankton. G. S. West in his report on the fresh-water Algæ of my expedition states (**200**, p. 96):—"Of the thirty species observed in this river-plankton, only one occurred in the plankton of the lake itself." This evidence is very suggestive, and appears to confirm the view put forward, as it is well known that the distribution of these delicate plant organisms is profoundly influenced by the nature of the water.

This is not perhaps the place to discuss at all fully what is known of the nature of the lake water, but the principal features may be indicated as follows. The total amount of dissolved saline matter is rather higher than in the case of Thames water, but is not excessive. The amount of calcium salts is, however, low, while salts of magnesium are present in much larger quantities than is characteristic of fresh waters. It is an obvious suggestion that the presence of this excess of magnesium salts—which are characteristically bitter to the taste—while not rendering the water unfit to drink, might be sufficient to affect these organisms and prevent them from obtaining a footing in the lake.

It becomes necessary in this connection to refer to the nature of the water of Lake Kivu, which is in direct communication with Tanganyika. Here the quantity of saline matter is excessive, and indeed most remarkable for a relatively large lake. From an analysis by Hundeshagen (**103**) it appears that while the water is almost entirely free of calcium salts, it contains a very unusual amount of salts of sodium and magnesium—particularly salts of magnesium, of which there are more than twice the amount present in Tanganyika.

The plankton of Kivu, among other lakes, was collected by the

German Central Africa Expedition of 1907–08, and Brehm, reporting on the Cladocera obtained by the expedition (**54**, p. 168), refers to the complete absence of these forms from Kivu, and expresses the opinion that the nature of the water may explain the fact. It seems, nevertheless, that a very occasional specimen may be found—presumably in the littoral zone,—for in the collection examined by Brehm was a tube labelled "Surface, Lake Kivu—one specimen *Alona*." This specimen he failed to find, but there is little doubt that such individuals must be carried into the lake by streams entering it. Indeed, the conditions are probably paralleled in Tanganyika, for not only does the existence of Cladocera in the Lofu River suggest this, but Sars (**151**, p. 67) actually observed an isolated specimen of *Moina* during his examination of plankton from the lake. Both these records I have purposely omitted from my list.

It only remains to suggest that since the river Rusisi, which is the outlet of Kivu, brings a considerable volume of water into Tanganyika, it is likely that Kivu is the principal source of the magnesium salts which appear to have an influence on the fauna of both the lakes in question.

It would be interesting, and should not prove difficult, to determine by experiment whether Cladocera are susceptible to the presence of small quantities of magnesium salts in the water, and, if so, whether they are affected by amounts too small to have any adverse influence on other Entomostraca*. Indeed, a whole field of experimental research is indicated, which might go some way towards determining whether the very special nature of the fauna of Tanganyika may not in some degree be related to the unusual nature and quantity of the salts dissolved in the water.

Turning from these matters to a survey of the list of Cladocera, it will be noted that 51 species in all have been enumerated. Of these, 31 species are recorded from Lake Victoria, 30 from Nyasa, 6 from Edward Nyanza, and only one from Albert Nyanza. It is interesting, though perhaps not surprising, to observe that an overwhelming majority of the forms were already known from other parts of the world, only 2 species out of 51 being described as endemic, to wit *Daphnia monacha* from Lake Albert and *D. kirimensis* from Lake Edward. A number of the forms are truly cosmopolitan and many more are known from two or three continents, while only four are restricted to other parts of Africa in addition to the lakes. On comparison with the particulars given for the Copepoda and Ostracoda, it becomes clear that while the former group holds an intermediate position, the Ostracoda are the most limited in range and the Cladocera the most extended. Of 44 species of Ostracoda enumerated, 33 are described as endemic in one or other of the lakes: out of 54 species of Copepoda, 30 are endemic: while out of 51 species of Cladocera only 2 are endemic. It can hardly be doubted that this is due to the exceptional facilities for distribution afforded by the thick-shelled "resting" eggs of the Cladocera.

---

* A brief reference is made by Gurney to his observations of the injurious effect of magnesium salts on the growth of fresh-water *Daphnia* (**97**, p. 469).

A detailed survey of the distribution of the genera in the lakes does not seem called for, but certain features may be pointed out. All the well represented and more important genera appear to occur in two or more of the lakes, while it is the less outstanding forms which are only known at present from one of the lakes in question. *Chydorus* and *Alona* are the best represented genera, each with 6 species, *Daphnia* and *Alonella* following closely with 5 species each. From Albert Nyanza, as already mentioned, there is only the record by Brehm (**54**, p. 169) of a single species of *Daphnia*. I have, however, in my possession a small quantity of plankton from the lake collected in July 1907 by my friend R. T. Leiper (*cf.* **74**), and though I have not yet found an opportunity of properly studying the Cladocera which it contains, I can at least indicate the occurrence of the genera *Diaphanosoma*, *Moina*, *Camptocercus*, *Alona*, and *Chydorus*. Having made no specific determinations, these new records are not included in my list of forms, but attention is merely called to them in this place. The addition of these genera to its fauna brings Lake Albert far more into line with Lake Edward and the larger lakes.

To sum up—Lakes Tanganyika and Kivu quite unexpectedly contain no Cladocera. This is very probably due to the salinity of the water, and perhaps in particular to the excess of magnesium salts in those lakes. Apart from this, the distribution of species in the lakes affords little of interest, many of the forms being cosmopolitan and only an insignificant number endemic.

BRANCHIOPODA.

Although representatives of this group have been found in various parts of the African continent, there is, as far as I am aware, only a single record which concerns the lakes under review. A species belonging to the family Estheridæ, viz. *Cyclestheria hislopi*, was collected by Fülleborn in the neighbourhood of Nyasa, though not actually in the lake itself (**76**, p. 159). This form, originally described as *Estheria*, but subsequently separated from that genus, is of wide distribution in the tropics, and its occurrence in the fauna of Lake Nyasa has no particular significance.

PENTASTOMIDA.

These parasitic Arachnids have not, I believe, been hitherto recorded from any African fishes. I obtained a number of specimens of *Porocephalus* from Tanganyika fish, encysted forms from the body-cavity and others from the intestine. The material has been submitted for expert examination, but no detailed report is yet available. Since the specimens came from very distinct hosts—a Siluroid in the one case and a large *Lates* (Serranid) in the other,—it may be they will prove to belong to different species. It is open to question whether such forms should be included in a description of lake faunas.

HYDRACHNIDA.

It is probable that the Hydrachnida of the great African lakes are but imperfectly known to science, although 31 species in all have been enumerated. Comparatively small and inconspicuous forms as these mites are, there seems little doubt that a good many more species will come to light in the future. Following on the earliest collections made by Stuhlmann, come those of Fülleborn in and around Nyasa and of Borgert in Victoria Nyanza. Specimens from both those lakes and also from Tanganyika were obtained by the expedition which I conducted in 1904–05. It seems likely that Lake Nyasa, from which the largest number of types (14) is on record, has been better explored in this direction than the remaining lakes. No Hydrachnids have hitherto been collected in either Albert Nyanza or Kivu.

Table of Distribution of Hydrachnida †.

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Edward Nyanza.	Other parts of the world.
Family HYDROPHANTIDÆ.					
Georgella incerta	...	...	P §	...	Quilimane, Nossi-Bé.
Diplodontus despiciens	P	...	...	...	Cosmopolitan.
Family HYGROBATIDÆ.					
Limnesia armata	...	E			
„ campanulata	...	E			
Anisitsiella africana	...	...	E §		
Hygrobates edentipalpis	E				
Oxus stuhlmanni	...	E			
Unionicula borgerti	...	E			
„ crassipes	...	P	...	...	Europe.
„ digitatus	...	...	P	..	Nossi-Bé.
„ falcifer	...	E			
„ figuralis	P	P	...	...	Europe.
„ lynceus	...	...	...	E	
„ cunningtoni	...	...	E		
Eucentridophorus borgerti	...	E			
„ koenikei	...	...	E §		
„ spinifer	...	P	P	...	Zanzibar.
Neumania paucipora	...	P	...	..	East Africa.
„ simulans	...	...	P §	...	Soudan, Quilimane.
„ spinipes	...	P	...	...	Europe.
„ papillosa	E				
Koenikea tessellata	...	...	E §		
Piona caligifera	...	...	P §	...	Madagascar.
„ rotundus	...	P	...	...	Europe.
Forelia liliacea	P	...	...	...	Europe.
Mideopsis minuta	E				
Arrhenurus plenipalpis	...	...	P	...	Madagascar, Quilimane.
„ sarcinatus	...	...	P §	...	Madagascar.
„ tæniatus	...	...	E §		
„ vigorans	...	...	P §	...	Nossi-Bé.
„ voeltzkowi	...	...	P §	...	Madagascar, E. Africa.
14 genera	6 P.	6 P.	8 P.	1 P.	
31 species	3 E, 3P. (6)	6E, 6P. (12)	5E, 9P. (14)	1E.	

† For additional information refer to Daday (**76**, p. 237) and Soar (**172**).

§ Not actually recorded from the lake itself, but from within its drainage area.

The distribution in the lakes of the forms at present recorded is made clear by the adjoining list of species, and it will at once be observed that the exceptional position held by Tanganyika in the case of other animal groups is not in evidence here. While the possibility is not excluded that further investigation may bring to light an unusual number of remarkable species in the lake, it is not in this group of animals that such a discovery is very probable. Nyasa with 14 different forms is closely followed by Lake Victoria with 12. Only 6 species are recorded from Tanganyika and one from Lake Edward. The number of species which are endemic affords no striking contrasts, 5 out of 14 being peculiar to Nyasa, and half the total number in each case being peculiar to Victoria and Tanganyika. The only species known from Edward Nyanza is endemic. There are no endemic genera on record.

A point of more interest is the fact that of 31 species mentioned in the table, only two have been observed in more than one lake, viz. *Unionicula figuralis* in Tanganyika and Victoria and *Encentridophorus spinifer* in Victoria and Nyasa. In every other case the species from the lakes differ from one another, and have been recorded only from a single lake, where, in some instances, they are endemic. Although this is so, there is not much evidence of that association of certain groups of forms with certain lakes, which is elsewhere a noticeable feature. It may, however, be pointed out that both species of *Limnesia* are recorded only from Lake Victoria, while all the species of *Arrhenurus* come only from Nyasa. Other genera well represented are *Unionicula* and *Neumania*, but they both have an extended range and have representatives in each of the three bigger lakes.

While 15 species in all are described as endemic, 10 of the remainder are known from other parts of Africa (including Madagascar) and 6 possess an even wider distribution. Under these circumstances there seems every probability that future exploration will prove many of the types to occur more generally in the lakes, though on the whole it may be predicted that in any case their precise distribution is little likely to afford evidence of a striking character.

TARDIGRADA.

It is not surprising that inconspicuous organisms belonging to this group have been seldom observed in the fresh-waters of Africa. Apart from a record of the existence of these forms in the Azores, there is, I believe, only the account given by Daday (**76**, p. 236) of specimens which Fülleborn collected in and around Lake Nyasa. The specimens in this collection all belong to the species *Macrobiotus tetronyx*, which Daday established to receive them. While this form must be regarded as endemic in Nyasa, the genus *Macrobiotus* is known to have a cosmopolitan distribution, so that the existence of this particular species in the lake is doubtless a matter of little import.

OLIGOCHÆTA.

It is necessary, in compiling an account of the Oligochæte worms from the lakes, to distinguish as far as possible between the purely aquatic and the purely terrestrial forms. Yet this is not a simple task, for not only are there a number of types which lie on the border-line, but even the true earthworms in the tropics are semiaquatic in habit, living in very wet places not far from water. For the purposes of this paper, the border line species as well as the true aquatics have been retained, those forms being excluded which are generally recognised as earthworms. It follows from what has been said, that even worms with specific names such as *tanganyikæ* have been omitted from the list when the name has been applied to a terrestrial species.

Aquatic Oligochæta are recorded from five out of the six lakes under review, but there is reason to suppose that a good many more records will be forthcoming. The list which follows gives the impression of being incomplete, yet it incorporates, I believe, all the available information. Since a number of these forms are small and inconspicuous, it is not unlikely that they have hitherto escaped notice. No species have been reported from Edward Nyanza. In a few cases, records have been inserted without specific determination. While these are unsatisfactory, they still have a certain value, as proving the occurrence of a particular genus.

Table of Distribution of Oligochæta †.

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Kivu.	Other parts of the world.
Family NAIDOMORPHA.						
Naidium sp.	...	P				
Nais sp.	...	...	P			
Dero sp.	...	...	P			
Aulophorus stuhlmanni	...	E				
Pristina longiseta	...	...	P	...		Europe, America.
Family ALLUROIDIDÆ.						
Alluroides tanganyikæ	P	...	...	...	...	Rhodesia.
Family MEGASCOLECIDÆ.						
Sub-family *Ocnerodrilinæ*.						
Ocnerodrilus (Ilyogenia) cunningtoni	E					
Pygmæodrilus affinis	...	E				
,, bipunctatus ...	...	...	...	P	P	E. Africa.
,, bukobensis ...	...	E				
,, grawerti	E					
,, kiwuensis	...	...	...	..	E	
Family GLOSSOSCOLECIDÆ.						
Subfamily *Criodrilinæ*.						
Alma emini...	...	E				
,, stuhlmanni	...	P	...	P	...	E. Africa.
9 genera	3 P.	4 P.	3 P.	2 P.	1 P.	
14 species	2 E, 1 P. (3)	4 E, 2 P. (6)	3 P.	2 P.	1 E, 1 P. (2)	

---

† The records of these forms from the African lakes are somewhat scattered in the literature of the subject. Refer especially to Beddard (**12 : 13**) and to Michaelsen (**120 : 121**), who gives a bibliography.

An examination of the table of distribution suggests in the first instance that there are certain gaps in the list which future investigation will surely fill. It is strange, for example, that no representatives of the Naidomorpha have been found in Tanganyika or in the smaller lakes, for it does not seem likely that they are entirely wanting. Secondly, it is clear that very few of the forms enumerated have been observed in more than one lake, half of them being classed as endemic. Out of a total of 14 species, the highest number recorded from a single lake is 6 (Victoria Nyanza).

There is no indication in this case of a marked pre-eminence for Tanganyika either in the number or peculiarity of its forms. Lake Victoria leads the way with 6 species, 4 of which are endemic, Tanganyika coming second, with exactly half that number (3 in all, 2 endemic). Lake Kivu also contains an endemic form. The species are distributed among a large number of genera (nine), only two of which—*Pygmæodrilus* and *Alma*—are represented by more than a single type. Lake Victoria again heads the list with representatives of four genera, Tanganyika and Nyasa coming next, each with three. No endemic genera occur.

It would serve no good purpose to review in detail the distribution of the different genera and species, but reference may be briefly made to the nature of the Oligochæte fauna of each lake. Tanganyika alone contains a member of the Alluroididæ. This worm—*Alluroides tanganyikæ*—was first described from Tanganyika, but has since been obtained from Rhodesia in the neighbourhood of the Victoria Falls. Two endemic species of Ocnerodrilinæ complete the list: there are no Naids or Criodrilines known.—In Victoria Nyanza the types are more uniformly distributed among the families concerned. Of four endemic species, two belong to the genus *Pygmæodrilus* and one each to *Aulophorus* and *Alma*.—From Nyasa only three Naid genera of wide range are on record. *Pristina longiseta*, which I collected in that lake, is the only worm in the list which occurs outside the continent of Africa, being known both from Europe and America. It is strange that other aquatic Oligochætes have not been forthcoming from this lake as a result of its careful exploration by Fülleborn.—Lakes Albert and Kivu each contain but two species. Two forms of *Pygmæodrilus* (one endemic) come from Kivu, with one *Pygmæodrilus* and an *Alma* from Albert. No Naids have so far been observed. These lakes, together with Lake Edward, have recently been visited by the German Central Africa Expedition, and it is, therefore, the more surprising that no Oligochæte worms have been found in Lake Edward.

HIRUDINEA.

There is but little known of the leeches which inhabit the great lakes of Central Africa: indeed, there appears to be only a single published record concerning them, which is that of

Blanchard (15) describing forms collected by Stuhlmann. It is in a measure surprising that these creatures should have escaped attention, since they are neither minute nor inconspicuous. During my expedition to the great lakes I was able to collect a considerable number of specimens, the majority of which were obtained in Tanganyika. Some examples, however, were found in Victoria Nyanza (from which a representative had already been recorded by Blanchard), and also in Nyasa, where they constitute a new record. With this opportunity for gaining a fuller knowledge of these forms, it is the more to be regretted that no report has yet been received from the expert to whom the collection was submitted for examination.

The leech which is already known from Lake Victoria was termed *Hirudo hildebrandti* by Blanchard (**15**, p. 5). It is not confined to the lake, specimens having been collected also in Mombasa. In the same paper a new genus and species belonging to the family Herpobdellidæ is described under the name of *Salifa perspicax*. This form was collected by Stuhlmann in Kiriwia, which is described as north-west of Edward Nyanza. I have not been able to identify this locality, but it appears doubtful whether this species should be included in the fauna of this or any of the lakes.

It is hardly safe to foreshadow the results of a proper examination of the specimens collected by the Third Tanganyika Expedition. It may nevertheless be stated that they will in all probability prove to belong to some five or six different species, of which the greater number come from Tanganyika. This is only in accordance with what has already been observed in so many animal groups. The leeches were found for the most part in shallow water, under stones or on shells, but some were dredged in about 10 fathoms.

NEMATODA.

There is hardly any information available concerning the Nematodes of the great lakes. In the extensive plankton material collected by Fülleborn in and around Nyasa, Daday detected certain free-living forms, which he identified and described. Reporting on Stuhlmann's collections, Collin records a single specimen of a free-living Nematode (which he leaves undetermined) from Victoria Nyanza, and also examples of a well-known parasitic type—*Ascaris spiculigera*—obtained from a pelican on Lake Edward (**64**, p. 10).

During my expedition to the three big lakes, I was able to procure a considerable number of parasitic Nematodes from the fish which passed through my hands. Whether such forms can be legitimately regarded as part of the lake fauna may be questioned, but as they are associated in this case with genuine inhabitants of the lakes, I am disposed to include them. Unfortunately these specimens have not been reported upon, so that little can be added to this bare record of their existence. The majority of them are from the body-cavity or gut of Tanganyik fishes, but some were obtained from a large Siluroid taken in Victoria Nyanza. In all, these parasites were collected from 8 different species of fish, belonging to 8 genera and 5 families. Since these fishes are, with a single exception, endemic forms, it is likely that their parasitic Nematodes will prove interesting and perhaps new to science.

It does not seem logical to regard the *Ascaris* from the Edward Nyanza pelican as belonging to the fauna of that lake, and as the specimens I collected have not been identified or described, the only records available for the purposes of this paper are those of the free-living types from Nyasa. The species *, which all belong to the family Anguillulidæ, may be enumerated as follows:—

1. *Monhystera fülleborni.*

Described as new from a single specimen in the surface plankton.

2. *Monhystera vulgaris.*

A species known previously only from Europe. Obtained near the mouth of a river which enters the lake.

3. *Monhystera similis.*

Likewise recorded from Europe and found in the neighbourhood of Nyasa.

4. *Trilobus graciloides.*

This species has been described as new by Daday. It comes from the vicinity of Nyasa, but has also been taken on the swampy shores of Lake Rukwa.

5. *Mononchus tenuis.*

Under this name Daday described a single male specimen which he found in a sample of mud brought from the bottom of Nyasa at a depth of 200 metres.

6. *Monochus macrostoma.*

Collected in a pool near the lake. Also known from Europe.

7. *Dorylaimus macrolaimus.*

A European species which appears to be common in the waters around Nyasa, but has not been observed in the lake itself.

Out of a total of 7 species, 2 may be regarded as peculiar to the lake fauna, while one of the remaining forms is confined to East Africa. The others are known also in Europe.

Thus there is no indication that the free-living Nematoda of Nyasa are in any way remarkable or specialised, and information is not available concerning either free-living or parasitic types from any of the other lakes.

---

* Particulars of these will be found in Daday's monograph (**76**, p. 44).

ROTIFERA.

The Rotifera of the African lakes are still very imperfectly known, and the table of distribution which follows probably gives quite an inadequate idea of the fauna. No information is available for Lakes Edward and Kivu, and very little for Lake Albert. Tanganyika, Victoria Nyanza, and Nyasa have been better, though very unequally investigated. The latter has been fairly well explored in this direction by the efforts of Fülleborn, who obtained numerous examples of the lake plankton and, in addition, suitable material from neighbouring ponds, swamps, and rivers. Tow-nettings from all three lakes were procured by my expedition, the largest series coming from Tanganyika, but with the single exception of samples taken in the broad mouth of the Lofu River, which enters Tanganyika, I did not collect outside the confines of the lakes themselves. Thus, while the truly lacustrine types from Nyasa and Tanganyika may be fitly compared, the Nyasa total is enormously swollen by species from the adjoining neighbourhood, whereas the region around Tanganyika remains almost entirely unexplored. In addition to my small collections from Victoria Nyanza, there have been those of Stuhlmann, Borgert, and Alluaud, but the Rotifera of the rivers etc., within its drainage area are likewise practically unknown.

Table of Distribution of Rotifera †.

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Other parts of the world.
Order PLOIMA.					
Notommata copeus	...	P§	...	...	Europe, Asia, N. America.
„ pachyura	...	...	P §	...	Europe, N. America.
„ tripus	...	...	P §	...	Cosmopolitan.
Pleurotrocha daphnicola	P §	...	...	...	Europe, N. America.
Cephalodella forficula	...	...	P §	...	Cosmopolitan.
Diaschiza forficata	...	...	P §	...	Europe, America.
„ gibba	...	...	P §	...	Cosmopolitan.
„ tigridia	...	...	P §	...	Europe.
Monommata orbis	...	...	P §	...	Europe, N. America.
Dicranophorus auritus	...	...	P §	...	Europe, Asia, N. America.
„ forcipatus ...	...	...	P §	...	Europe, Asia, N. America.
Encentrum caudatum	...	...	P §	...	Europe, N. America.
Epiphanes oblonga	...	...	E §		
„ clavulatus	...	P	...	...	Europe.
„ lotos	...	...	P §	...	Asia.
„ brachionus spinosus	...	...	P §	...	Europe, S. America.
„ ? macrourus	...	P	P	...	Asia Minor.

---

† The principal sources from which this table has been compiled are Rousselet (**150**), Collin (**64**), and Daday (**76**, p. 59), where further particulars will be found. It is well to explain that the names under which the species are enumerated are mostly those adopted by Harring in his "Synopsis of the Rotatoria", Washington, 1913.

§ Not actually recorded from the lake itself, but from within its drainage area.

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Other parts of the world.
Brachionus angularis	...	P	P §	..	Cosmopolitan.
„ „ caudatus	...	P	P §	...	Rhodesia, N. America.
„ calyciflorus	P	P	P	...	Cosmopolitan.
„ „ dorcas	...	...	P	...	Europe, N. America.
„ capsuliflorus	...	...	P §	..	Cosmopolitan.
„ „ bidentatus	...	...	...	P	Asia, Europe.
„ falcatus	...	P	P	...	Cosmopolitan.
„ forficula	..	P	...	...	Europe.
„ mirabilis	...	...	P §	...	New Guinea, S. America.
„ patulus	P §	P	P	...	Cosmopolitan.
„ quadridentatus	...	P	P	...	„
„ urceus	...	P	P §	...	„
Platyias quadricornis	P §	P	P §	P	„
„ „ brevispinus	P §	...	...	...	Asia, S. America.
Schizocerca diversicornis homoceros	...	P	...	...	Europe.
Keratella cochlearis	...	P	P §	...	Cosmopolitan.
„ quadrata	P	P	P	...	„
„ „ valga	P §	P	P	P	„
Notholca striata labis	...	...	P	...	„
Anuraeopsis fissa	...	...	P §	...	„
Mytilina compressa	...	...	P §	...	Europe, N. America.
„ mucronata	...	...	P §	...	Cosmopolitan.
„ „ spinigera	...	...	P §	...	Europe, Asia.
„ ventralis	P §	...	P §	...	Cosmopolitan.
„ „ brevispina.	P	...	P	...	„
Euchlanis dilatata	...	...	P §	...	„
„ oropha	P §	...	...	...	Europe, N. America, Australia.
„ triquetra	...	...	P §	...	Cosmopolitan.
„ „ hyalina	P §	...	...	...	Europe.
Dipleuchlanis propatula	P §	P §	...	...	Europe, N. America, Asia.
Lecane gissensis	...	...	P	...	Europe, N. America.
„ lipara	...	...	P §	...	Europe.
„ luna	P	...	P §	...	Cosmopolitan.
„ leontina	P §	...	P §	...	Asia, America.
„ lofuana	E §				
„ ungulata	P §	...	P §	...	Europe, N. America, Asia.
Monostyla bulla	P	P	P	P	Cosmopolitan.
„ lunaris	P §	P	P §	...	„
„ hamata	...	...	P §	...	Europe, America.
Lepadella ovalis	...	...	P	...	Cosmopolitan.
„ acuminata	...	...	P §	...	„
„ cristata	...	...	P §	...	Europe, N. America.
„ patella	...	...	P §	...	Cosmopolitan,
Colurella colura	...	...	P §	...	Europe, N. America, Australia.
„ adriatica	...	...	P §	...	Europe, Asia.
„ bicuspidata	...	...	P §	...	Cosmopolitan.
„ deflexa	...	...	P §	...	Europe, America.
„ uncinata	...	...	P §	...	Europe.
Trichotria pocillum	...	...	P §	...	Cosmopolitan.
Scaridium longicaudum	...	...	P §	...	„
Pedalia mira	...	P	P	...	„
Filinia longiseta	...	P	P §	...	„
Tetramastix opoliensis	...	P	P	...	Europe, Rhodesia.
Trichocerca bicristata	P §	...	...	...	Europe, Asia, N. America.
„ cristata	...	...	P §	...	Cosmopolitan.

§ Not actually recorded from the lake itself, but from within its drainage area.

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Other parts of the world.
Trichocerca elongata	...	...	P §	...	Cosmopolitan.
" iernis	P §	...	...	...	Europe, N. America.
" longiseta	P §	...	...	...	Cosmopolitan.
" macera	P §	...	...	...	Europe, N. America.
" rattus	...	...	P	...	Cosmopolitan.
" scipio	...	...	P §	...	"
" stylata	P	...	P	...	Europe, S. America.
Diurella stylata	...	...	P	...	Europe, N. America.
" tenuior	...	...	P §	...	Cosmopolitan.
" tigris	...	...	P §	...	"
Synchæta oblonga	P §	...	P §	...	Europe, N. America, Australia.
" pectinata	...	...	P	...	Cosmopolitan.
" tremula	...	...	P §	...	"
Polyarthra trigla	P	...	P	...	"
Sphyrias lofuana	P §	...	...	...	N. America.
Asplanchna brightwellii	...	P	P	...	Europe, N. America, Australia.
" intermedia	P	...	...	..	Europe, N. America.
Asplanchnopus multiceps ...	...	...	P §	...	Cosmopolitan.
Testudinella patina	...	...	P §	..	"
" trilobata	P §				Australia.
Order Rhizota.					
Floscularia ringens	...	...	P §	...	Cosmopolitan.
Limnias melicerta	...	...	P §	...	"
Ptygura mucicola	P §	...	...	...	N. America.
Sinantherina spinosa	...	...	P §	...	Cosmopolitan.
Conochilus hippocrepis	...	...	P §	...	"
Collotheca ornata	...	...	P	...	Europe, N. America, Australia.
Order Bdelloida.					
Philodina citrina	...	...	P §	...	Cosmopolitan.
" emini	...	E §			
" roseola	...	...	P §	...	Cosmopolitan.
Rotifer macroceros	...	...	P §	...	"
" macrurus	...	...	P §	...	"
" vulgaris	...	P §	P §	...	"
" actinurus	...	...	P §	...	"
42 genera	16 P.	13 P.	37 P.	4 P.	
105 species and subspecies...	1E,28P. (29)	1E,24P. (25)	1E,84P. (85)	4 P.	

§ Not actually recorded from the lake itself, but from within its drainage area.

Attention has already been called to the fact that the Rotifera of Nyasa are in all probability better known than those of the other lakes. Of 105 forms enumerated, 85 are reported from that lake, while only 29 are given for Tanganyika, 25 for Victoria Nyanza, and 4 for Albert Nyanza. Examination of the Nyasa records shows that a much smaller total has been observed in the lake proper, and indeed it is the latter figure, compared with corresponding figures from the other lakes, which affords a truer basis of comparison than those given above, since the forms collected from the surrounding neighbourhood are almost unknown except for Nyasa. Disregarding Albert Nyanza—from which information is very meagre,—the totals of those Rotifers taken within the limits of the lakes themselves are found to be:—Nyasa 22, Victoria Nyanza 21, and Tanganyika only 8. Clearly there is little disproportion between Lakes Victoria and Nyasa, but Tanganyika shows a marked reduction in number. It is probable that the low figure for Tanganyika proper has some relation to the nature of the lake water, which appears to be somewhat unsuited to these organisms. Rousselet points out in his report on my collections (**150**, p. 794) that there is a striking difference between the scanty Rotiferan fauna of the lake and the far richer fauna which he observed in a small quantity of material from the Lofu River. Tanganyika water contains an unusual amount of magnesium salts, and though very little is really known concerning the influence of such salts on fresh-water organisms, this seems likely to be the cause of the dissimilarity between lake and river in this respect. The matter has already been discussed in some detail in connection with the complete absence of Cladocera from the lake (*cf.* p. 569).

On examining the list of Rotifera more closely, it will be observed that with three exceptions, the forms are all known from other parts of the world, many of them, in fact, being cosmopolitan in their distribution. A single endemic species is enumerated from each of the three bigger lakes, but apart from *Lecane lofuana* described from the Lofu River, these are of only doubtful value. The facilities for dispersal which the Rotifers possess are well known, and quite account for this wide distribution. In the case of these organisms, therefore, no deductions of any value can be made from the presence or absence of a species in a particular lake, and the interest attaching to a comparative table of distribution is, in consequence, small.

Nor does a study of the actual genera and species occurring disclose features of much significance, although one or two comments may be offered. In all, 42 genera are enumerated, of which again the largest number is found in Nyasa. Those best represented are *Brachionus* with 12 species, or well-marked varieties, *Trichocerca* with 9 and *Lecane* with 6, while nearly all the more important genera are known from at least two of the lakes. Certain cosmopolitan species have been identified from all the four lakes under consideration. There is little to note in the way of unexpected forms or of types unaccountably absent. A subspecies of *Brachionus*—*B. capsuliflorus bidentatus*,—which was isolated from the Albert Nyanza material, is apparently very rare, having been observed only in Calcutta and more recently in Bulgaria. Furthermore, Rousselet has pointed out that the genus *Asplanchna* is recorded from the lakes, but has not been obtained in South Africa.—In conclusion, it will be observed that as in the case of the Cladocera—which are also of extended distribution,—there is no indication of an exceptional fauna peculiar to Tanganyika, or indeed to any of the lakes.

Gastrotricha.

Representatives of this group may eventually prove to be widely distributed in the African lakes, but at present there is little information at hand concerning them. An account of certain forms collected by Stuhlmann at Bukoba, Lake Victoria, is given by Collin (**64**), while other species which Fülleborn obtained in the neighbourhood of Nyasa have been identified by Daday (**76**, p. 56). No Gastrotricha were observed by me during my expedition to the great lakes. The species* may be enumerated as follows:—

1. *Lepidoderma squamatum.*

A species well known in Europe and occurring also in North America. A single specimen was collected in a pool near the shores of Nyasa.

2. *Lepidoderma hystrix.*

Under this name Daday described a form obtained from the same locality as the above. It has not been observed elsewhere.

3. *Ichthydium macrurum.*

This type was described as new by Collin, but the species rests upon a diagrammatic figure and a very incomplete description. It was found at Bukoba, a station on the shores of Victoria Nyanza, and has not been re-discovered, so that it may be looked upon as a species of rather doubtful value.

4. *Chætonotus formosus.*

This form, like the two species of *Lepidoderma*, has been identified from the vicinity of Lake Nyasa. Previous to this discovery it was only known from North America.

5. *Chætonotus pusillus.*

A single specimen of this type, hitherto only recorded from Paraguay, was isolated by Daday from material collected in the Mbasi River close to its entrance into Nyasa.

Two species of *Chætonotus* are, according to Collin, among the Gastrotricha which Stuhlmann recorded from Lake Victoria, but in neither case has it been possible to identify them further. Brief notes made on the spot, accompanied in one case by a sketch, form all the information available. It is doubtful whether either of these types was observed in water from the lake itself.

6. *Gossea pauciseta.*

Another species previously known only from Paraguay. Several specimens of this were obtained from a pond in the Nyasa district.

On a survey of this list the following facts appear. Five species are on record from Nyasa, one of which is peculiar to that lake. From Victoria Nyanza three different forms have been reported, of which one was described as new and has not been found elsewhere. The two remaining types were not specifically identified, and indeed all three species from this lake rest on a somewhat insecure basis. None of the recorded species occur in both Victoria and Nyasa, and it appears probable that none were actually observed in the waters of the lakes themselves. No Gastrotricha are known at present from any of the other African lakes.

---

* For further particulars of these forms, consult Collin (**64**, p. 9) and Daday (**76**, p. 56).

TURBELLARIA.

There can be little doubt that Turbellarians are relatively uncommon in the lakes as well as in other parts of Central Africa. Stuhlmann, a careful observer, who had opportunities for collecting in many parts of the country, remarks on the scarcity of these organisms, and in particular on the scarcity of the fresh-water Dendrocœls, which are usually common in ponds and streams (**181**, pp. 1262 & 1268: **182**, p. 652: **185**, p. 349). During my expedition to the great lakes, I only observed Turbellarians in Tanganyika. They were found on the under side of stones in shallow water, and all proved to belong to a single species of the well-known genus *Planaria*. Prior to the description of this Tanganyikan form by Laidlaw (**107**), the only work dealing with species from the lakes was that of Böhmig (**17**), who reported on the collections made by Stuhlmann. Unfortunately, the accounts in this paper are based almost entirely on sketches and notes made on the spot, which often lack details of importance for systematic determination. Although the records must thus be regarded as of doubtful value, I insert them here without further comment. The following species * come within the scope of this survey :—

1. *Planaria tanganyikæ.*

This is the type from Tanganyika to which reference has been made. It is the only species known from that lake and has not been obtained elsewhere.

2. *Stenostoma leucops.*

A form known in Europe and also in North America. On the evidence of drawings, recorded from the neighbourhood of Bukoba, on Victoria Nyanza.

3. *Stenostoma stuhlmanni.*

Described as new by Böhmig from Stuhlmann's notes and sketches. Observed at Bukoba, Lake Victoria and unknown elsewhere.

4. *Stenostoma gilvum.*

Another species based only on a drawing and a few notes and recorded from the same locality as *S. stuhlmanni*. Nothing further is known of this form.

---

* For details, consult the above-mentioned papers: Böhmig (**17**) and Laidlaw (**107**).

Examples of two species of *Stenostoma* from Bukoba were among the material examined by Böhmig, but their unfavourable state of preservation did not permit of nearer identification.

5. *Gyrator hermaphroditus.*

A pelagic Turbellarian collected in Victoria Nyanza is identified with this species by Böhmig. It is well known in Europe.

6. *Vortex quadridens.*

This type is established merely on the evidence of sketches and notes by Stuhlmann. It is admitted that certain important features of the genital apparatus are unknown. Obtained from stagnant water at Bukoba.

From the above it will be observed that Turbellaria are only recorded at present from Lakes Victoria and Tanganyika. From Victoria Nyanza and its neighbourhood five forms have been specifically identified, three of them being peculiar to the lake. There are, in addition, two types which are unnamed. These records of Böhmig, however, need confirmation, as they are based on very meagre evidence. From Tanganyika a single endemic species is known, which belongs to the widely distributed genus *Planaria* *. No doubt further representatives of this group will eventually be found in the great lakes, but they appear to be less common than might have been expected. There is no suggestion of a striking Turbellarian fauna in Tanganyika and little indication that such will be discovered in the future.

TREMATODA.

Practically nothing is known of the distribution of these exclusively parasitic animals in the lakes of Africa. Following the argument advanced in the section dealing with the Nematoda, it seems only logical to include such forms in a lake fauna. In the case of these organisms they may be obtained in the free-swimming larval stage, or infesting an intermediate Molluscan host or in their final vertebrate host. As far as I am aware, the description given by Daday (**76**, p. 39) of two Cercaria larvæ from the neighbourhood of Nyasa is the only account which concerns any of the lakes. Both were found in material from ponds near Nyasa and were described as new larvæ, though it seems doubtful whether such determinations have much systematic value. They have received the names of "*Cercaria*" *schizocerca* and "*Cercaria*" *hoplophora* **76**, p. 288).

---

* It seems clear that Stuhlmann's statement that Planarians cannot survive temperatures of over 25° C. (**185**, p. 349) is not universally true. The specimens I collected in Tanganyika were taken in quite shallow water, where the temperature tends to be highest, yet my thermometer readings for the surface of the lake showed a higher average than 25°.

In the course of my expedition I collected in Tanganyika a few Trematodes which are parasitic on fish. They constitute a new record for this lake, but have not yet been examined and described. The specimens were taken from large Siluroids, in one case from the gill-arches, in another from the gut.

CESTODA.

As far as I have been able to ascertain, no records have been published of tape-worms from the lakes included in this survey, although Daday described two new larvæ which he observed in East African Copepods. Different forms of tape-worm proved common in the gut of fishes examined for parasites by my expedition, and I succeeded in getting a considerable number of specimens. These all came from Tanganyika, where I had better opportunity than elsewhere to seek such organisms, but it is clear that systematic examination would not only bring to light enteric parasites from the fishes of other lakes, but would result in a far richer series from Tanganyika. My material has only received a preliminary examination, so that little information can yet be given as to the nature of the Tanganyika forms. A species which occurred abundantly in an endemic Siluroid proves to be one of the unsegmented Cestodes, and has been referred to the genus *Caryophyllæus*. It has not been more fully identified. Almost all the remaining specimens come likewise from endemic fishes belonging to different genera of Cichlids and Siluroids. Thus it is quite probable that other species of tape-worm—perhaps new forms—are represented in the collection. It is to be hoped that the investigation will shortly be completed.

CŒLENTERATA.

The only representatives of this group at present recorded are the common fresh-water *Hydra* and the medusa which so stimulated interest in the fauna of Tanganyika. Stuhlmann obtained specimens of *Hydra* from Victoria Nyanza which resemble the common *H. fusca*, though Weltner, reporting on this material, would not venture to identify the species in the absence of eggs (**199**, p. 2). *Hydra* has never been discovered in any of the other lakes so far as I am aware, which is perhaps rather strange.

The Tanganyika medusa was described by R. T. Günther under the name of *Limnocnida tanganicæ* * (**94**), and being peculiar to the lake, was, of course, regarded by Moore as one of the most striking halolimnic or relict forms. The significance of its occurrence in this lake in the heart of Africa, which communicates with the sea only by some thousand miles of river, broken by falls and rapids, was obvious, especially since the number of fresh-water medusæ then known was very small. Discoveries made since Moore's expeditions, however, have put a very different complexion on the matter. Fresh-water jelly-fishes of other types have been found in the Yang-tse Kiang, in a lake in Egypt and in the Caspian. Moreover, the distribution of the genus *Limnocnida* itself has proved wider to an unforeseen extent. In August 1903 a medusa was discovered in the great Kavirondo Gulf of Victoria Nyanza and another in a fresh water lagoon in the Niger delta. The specimens from Lake Victoria were submitted to Günther, who pronounced them indistinguishable from the Tanganyika species, though he subsequently modified his view, and described them as *L. tanganicæ* var. *victoriæ* (**96**, p. 651). The Niger medusæ were reported on by E. T. Browne, who considered them undoubted specimens of *L. tanganicæ* (**55 : 57**). In 1908, medusæ were found in a tributary of the Zambezi. These were regarded by C. L. Boulenger as specifically different from the Tanganyika form, and were named by him *Limnocnida rhodesiæ* (**18**, p. 429). The latter species has still more recently (1913) been obtained from another part of Rhodesia, where it occurred in a tributary of the Limpopo River (**11**). Remarkable as it was to find this genus so widely distributed in Africa, the discovery of a species in India in 1911 was more remarkable still (**6**). This type, which comes from streams in the Western Ghats, differs slightly from the African species, and was termed *L. indica* by Annandale (**9**).

---

* The specific name is that of Böhm, the discoverer of the medusa, who wrote it "*tanganjicæ*." I follow Günther (**96**, p. 651) and most subsequent writers in adopting *tanganicæ* as a more rational spelling.

The bearing which these discoveries have on the problem of the origin of the Tanganyika fauna, needs little pointing out. There can be no hesitation in deriving medusæ from the ocean, and when Tanganyika was believed to be the only locality in the whole continent in which such organisms occurred, the lake was naturally regarded as unique, and the medusæ were looked upon as strong evidence in favour of a marine origin for its fauna. In the light of present knowledge, this evidence becomes greatly weakened. If *Limnocnida* is to be regarded as a relict form, it has now attained so wide a distribution that its presence no longer singles out Tanganyika as a probable "Reliktensee." Moreover, it must be noted that the new records are none of them from the basin of the Congo, where the medusa should be forthcoming in accordance with Moore's view of the origin of the lake.—The finding of a species of *Limnocnida* in India affords another example of those Afro-Indian affinities to which reference has more than once been made.

It will be more satisfactory to postpone a consideration of the sources from which the medusa may have been derived, until the general discussion—which will follow this systematic account—of the zoological and of other evidence.

PORIFERA.

Representatives of this group are known at present only from the three largest of the six lakes under consideration. Since however, fresh-water sponges are usually inconspicuous objects, it is very probable that sooner or later specimens will be found in the other lakes*, although Schubotz states that he completely failed to find any in Kivu (**156**, p. xiv). The species from Victoria Nyanza and Nyasa are quite ordinary forms, but those known from Tanganyika exhibit divergences of at least specific rank from the types collected in any other part of the continent. Of the eight species enumerated in the adjoining table, seven belong to the cosmopolitan fresh-water genus *Spongilla*, the eighth—about which doubts have been raised—being referred provisionally to the genus *Potamolepis*.

Table of Distribution of Porifera †.

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Other parts of the world.
Family SPONGILLIDÆ.				
Spongilla biseriata ……	…	…	P	Egypt.
„ böhmii ……	P §	…	..	E. Africa.
„ carteri ……	…	P	…	Hungary, India, Java.
„ cunningtoni …	E			
„ moorei ……	E			
„ nitens ……	P §	…	…	White Nile.
„ tanganyikæ …	E			
Potamolepis weltneri …	E			
8 species …………	4 E, 2 P.	1 P.	1 P.	

§ Not actually recorded from the lake itself, but from within its drainage area.

The distinctness of the fauna of Tanganyika is once more exemplified in the case of the sponges, and is shown graphically by the above list. While Victoria Nyanza and Nyasa each contain a single species of somewhat extended distribution, Tanganyika contains six other types, four of them (those occurring in the waters of the lake itself) being endemic.

The forms from Lake Victoria and Nyasa, both of which were obtained for the first time by my expedition, do not call for much comment. *Spongilla carteri*, now known from Victoria Nyanza, is the only sponge from the lakes to occur outside the continent of Africa. While it occurs in Europe, its occurrence also in India and Java is noteworthy in view of the affinities of other African and Indian types to which reference has already been made. Five species of *Spongilla* have been recognised from the Tanganyika area, three of them—all endemic—from the lake proper, and the remainder from the Ugalla River, a tributary of the Malagarasi, which in its turn enters the lake. The forms from the Ugalla River, *S. böhmii* and *S. nitens*, occur also in other parts of Africa. Following the usual procedure, from which it is perhaps illogical to depart, these species are inserted with an explanatory footnote in the Tanganyika column, but it may be pointed out that the district from which they come is some 200 kilometres or more east of the lake, and that they show East African rather than Tanganyikan affinities.

---

* Sponge spicules were observed by West in tow-nettings made in Albert Nyanza (**201**). It is probable that these occurred in the sample obtained from near the bottom in about 30 feet of water.

† The principal source of information on this group has been Kirkpatrick (**105**), where references to other authors are given.

The last of the forms enumerated *Potamolepis weltneri*—was established by Moore (**137**, p. 323), and regarded by him as peculiar to Tanganyika. Moore explains that a small specimen of this sponge was dredged in the lake from great depths during his second expedition *. It has never been adequately examined and described, but Weltner expressed the opinion that it was a distinct species, with a framework very similar to that of *Spongilla böhmii*. It was accordingly given the specific name *weltneri* and placed provisionally in the genus *Potamolepis*. Kirkpatrick, who has also examined some of the material, expresses the view that these two species may possibly be synonymous (**105**, p. 222). It is perhaps well to leave the matter *sub judice*, particularly as no further supply of material has been forthcoming to aid in deciding this point. Moore's comparison of the spicules of this sponge with those of the genus *Reniera* (which he misquotes "*Renieria*") does not strengthen his case. Instead of being "the old fossil genus" (*loc. cit.* pp. 331 : 354) it would be more accurately described as the recent marine and brackish-water genus—although fossil representatives also exist in the tertiary strata. In conclusion it may be stated that despite the suggested resemblance of the spicules of *Potamolepis weltneri* to those of *Reniera*, the sponge fauna of Tanganyika consists essentially of fresh-water and not marine types, although the forms inhabiting the lake are peculiar to its waters.

PROTOZOA.

It is to be regretted that the Protozoa of Tanganyika have not yet been investigated. There are, it is true, a few species to record, but these are principally forms belonging to the Phytoflagellata, which are enumerated in the report on the Algæ of my expedition (**200**). This is the more unfortunate, since a good deal of information on this group is forthcoming respecting Victoria Nyanza and Nyasa, although much is probably unknown. There is no reason to suppose that such a marked disproportion really exists between the Protozoan fauna of Tanganyika and those of the two other big lakes; indeed, the evidence afforded by many groups of animals suggests that Tanganyika is likely to lead the way with a larger and more unusual assemblage of species. An examination by a protozoologist of the extensive series of townettings and other suitable material which I brought from the lake should go some way towards determining this point, and it is to be hoped that this will be carried out in the near future. From Albert Nyanza there are a few forms recorded among the

---

* It may be mentioned in this connection that the species obtained by Moore's first expedition were, through some misunderstanding, said by Evans to have come from a depth of 350 fathoms (**82**, p. 471). Moore himself states (**127**, p. 405) that on this expedition 1200 feet (200 fathoms) was the greatest depth at which he was able to dredge. These sponges are not in reality deep-water forms, for, during the third expedition, I found them living in quite shallow water at the lake margin

Phytoplankton, and from Edward Nyanza a single species of Rhizopod, but it is obvious that these lakes too are quite unexplored as yet. Nothing is known of the Protozoa of Kivu.

Table of Distribution of Protozoa †.

Name of Species.	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Other parts of the world.
Class RHIZOPODA.						
Order Lobosa.						
Amœba proteus	...	P	...	...	...	Cosmopolitan.
Arcella apicata	...	P	...	...	...	E. Africa.
,, dentata	...	...	P §	...	...	Cosmopolitan.
,, discoides	...	P §	P	...	...	Europe, N. America, Australia.
,, jeanneli	...	E				
,, mitrata	...	P	P §	...	...	Europe, N. America.
,, vulgaris	...	P	P	...	...	Cosmopolitan.
? Hyalosphenia papilio	...	P	..	...	...	Europe, N. America.
Quadrula symmetrica	...	P	P §	...	..	Europe, N America.
Difflugia acuminata	...	...	P §	...	...	Cosmopolitan.
,, constricta	...	...	P §	...	...	Europe, N. America.
,, corona	...	...	P	...	...	Europe, N. America.
,, globulosa	...	P	P	...	...	Cosmopolitan.
,, limnetica	...	P	...	...	...	Europe.
,, lobostoma	...	...	P §	...	..	Cosmopolitan.
,, pyriformis	...	P	P	...	...	Cosmopolitan.
,, urceolata	...	..	P	..	...	Europe, N. America, Australia.
Centropyxis aculeata	...	P	P	...	..	Cosmopolitan.
Nebela carinata	...	...	...	...	P	Europe, N. America.
,, collaris	...	P	P §	...	...	Europe, N. America, Asia.
,, lageniformis	...	P	...	...	...	Europe, N. America.
Lecquereusia spiralis	...	P §	P §	...	...	Cosmopolitan.
Euglypha alveolata	...	P §	...	...	...	Cosmopolitan.
,, ciliata	...		P §	...	...	Europe, N. America, Australia.
Trinema enchelys	...	P	P §	...	...	Cosmopolitan.
Cyphoderia ampulla	...	P	P §	...	..	Europe, N. America.
Order Heliozoa.						
Actinosphærium eichhornii	..	...	P §	...	...	Cosmopolitan.
Raphidiophrys elegans	...	P	...	...	...	Cosmopolitan.
Clathrulina stuhlmanni	...	P	...	...	...	East Africa.
Class MASTIGOPHORA.						
Order Euflagellata.						
Euglena acus	...	...	P §	...	...	Cosmopolitan.
,, spirogyra	...	...	P §	...	...	Cosmopolitan.
,, viridis	...	P	P	...	..	Cosmopolitan.
Colacium calvum	...	...	P	...	...	Europe.
Trachelomonas annulata	...	...	P §	...	...	S. America.
,, hispida	...	...	P §	...	...	Cosmopoliton.
,, ovalis	...	...	E §			
,, volvocina	...	...	P §	...	...	Cosmopolitan.
Lepocinclis ovum	..	...	P §	...	...	Europe, Australia.
Phacus longicaudus	...	...	P §	...	...	Europe, Asia, America.
,, pleuronectes	.	...	P §	P	...	Cosmopolitan.
Pandorina morum	...	P	P	...	...	Europe, Asia, America.

---

† The majority of these records will be found in the accounts given of East African forms by Schaudinn (**154**) and Daday (**75 : 76**, p. 6), where further particulars are given.

§ Not actually recorded from the lake itself, but from within its drainage area.

Name of Species.	Tangan-yika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Other parts of the world.
Eudorina elegans	...	...	P	...	...	Europe, Asia.
Volvox africanus	...	...	...	P	..	E. Africa.
„ aureus	...	...	P §	...	...	Europe.
„ globator	...	...	P §	...	...	Europe, Asia, America.
Order DINOFLAGELLATA.						
Ceratium brachyceros	...	E				
„ hirundinella	...	P	...	..	...	Cosmopolitan.
„ macroceros	...	...	P	..	.	Europe, Asia.
Peridinium africanum	P	..	P			
„ berolinense.........	P	...	..	...	...	Europe.
„ inconspicuum ...	...	...		P	...	Cosmopolitan.
„ palatinum	..	...	P §	.	...	Europe.
„ quadridens.........	...	..	P	...	...	Europe, Asia, S. America.
„ tabulatum	..	...	P	.	...	Cosmopolitan.
Peridiniopsis cunningtonii ...	E					
Glenodinium pulvisculus ...	P	P	...	P	...	Europe, Australia.
Class CILIATA.						
Order CILIATA VERA.						
Enchelyodon farctus	..	...	P	.	...	Europe, N. America.
Coleps hirtus	...	..	P §	.		Cosmopolitan.
Loxophyllum meleagris	.	...	P	...	...	Europe, N. America.
Trachelius ovum	...	...	P	...	...	Cosmopolitan.
Dileptus anser	...	...	P	...	...	Europe, America, Australia.
Nassula sp.	..	P				
Colpidium sp.	P					
Paramœcium aurelia	..	...	P §	..		Cosmopolitan.
Spirostomum ambiguum	...	P	...	...	..	Cosmopolitan.
Condylostoma sp.	P					
Stentor roeselii	...	P	...	.		Europe, America.
Tintinnopsis ovalis	...	..	P		..	Europe.
Uronychia paupera	...	...	E §			
Trichodina sp.	P					
Vorticella lunaris	...	...	P §	...	..	Europe, N. America, Australia.
„ microstoma	...	P	P	...	.	Cosmopolitan.
„ nebulifera	...	P	P §	..	.	Europe, America, Australia.
Zoothamnium arbuscula	...	...	P §	...	..	Europe, America.
„ parasita	...	...	P §	...	...	Europe.
Epistylis anastatica	...	P	P §	...	..	Cosmopolitan.
„ brevipes	...	..	P	..	...	Europe, S. America.
„ plicatilis	...	...	P §	...	.	Europe, N. America.
„ umbellaria	...	P	P §	...	...	Europe.
Opercularia nutans	...	P	...	...	...	Europe, America, Australia.
Cothurnia crystallina	...	P	P §	...	...	Cosmopolitan.
„ incisa...	...	E				
„ lobata	...	E				
Order SUCTORIA.						
Podophyra sp.	...	P				
Tokophyra cyclopum	...	...	P §	...	..	Europe, N. America.
Acineta symbiotica	...	...	P	...	...	E. Africa.
„ tuberosa	...	...	P §	...	...	Europe, Asia.
48 genera	6 P.	25 P.	34 P.	4 P.	1 P.	
87 species	1E,6P. (7)	4E,33P. (37)	2E,58P. (60)	4 P.	1 P.	

§ Not actually recorded from the lake itself, but from within its drainage area.

The most obvious comment on the table of distribution is the great inequality in the totals recorded from the biggest lakes—an inequality which is obviously due in this instance to unequal investigation. Of the 87 species enumerated, 60 occur in Nyasa, 37 in Victoria Nyanza, and only 7 in Tanganyika. While it is impossible to predict what figures will be forthcoming when the Protozoa of the lakes are better known, the figures at present available are merely an index of this disproportionate investigation. The records from Nyasa are the result of the extensive collections made by Fülleborn, which were reported on by Daday (**76**). It will be noticed that more than half the species identified were not obtained in the lake itself, but came from river mouths, pools, and swamps in the vicinity. Victoria Nyanza has been less adequately explored in this direction, smaller collections being made by Stuhlmann and more recently by Borgert and others.

In his book on the Tanganyika Problem, Moore devotes a few paragraphs to the Protozoa of the lake (**137**, p. 323). The two forms which he mentions by name—a *Condylostoma* and a large Infusorian which he refers with some hesitation to the genus *Colpidium*— have been inserted in the table of distribution. He describes the latter organism as the cause of the yellow clouds which occur on the surface at times and make the water appear "as if tinged with a fine golden dust." This effect was also observed by Livingstone, who thought the yellow scum to be of vegetable origin. I have repeatedly observed the phenomenon myself, not only on Tanganyika, but on Nyasa, and without denying other possibilities, I can confidently assert that it is usually due to limnetic Algae. In conclusion, Moore remarks that he found some twenty types of Protozoa belonging to groups common in tropical fresh-waters.

A consideration of the list of species shows that in the great majority of cases the forms are widely distributed if not cosmopolitan in range. There are very few endemic species enumerated—four in Lake Victoria, two in Nyasa, and one in Tanganyika—and most of these are of little interest. *Peridiniopsis cunningtonii* from Tanganyika, and *Uronychia paupera* from Nyasa, are perhaps of more interest, since in each case they are only the second described species of the genus. Forty-eight genera are mentioned in the table of distribution, of which the greatest number occur in Nyasa. This is a large proportion of genera to species, but is accounted for by the number of genera represented by only a single species. None of the genera are endemic.

No good purpose would be served by commenting in detail on the genera and species in the list, but one or two further remarks on their distribution may be offered. As far as the Rhizopoda are concerned, the lists from Victoria Nyanza and Nyasa may be reasonably compared, and they exhibit a close degree of similarity. The well-known genera *Arcella* and *Difflugia* are each represented by a number of species. It is in the remaining groups that there has been inequality of investigation, so that the Euflagellata, for example, are only represented in Lake Victoria by a couple of forms as contrasted with a large number from Nyasa. *Volvox africanus* is an interesting species which was established to receive specimens brought by Leiper from Albert Nyanza. It can no longer be regarded as endemic, since it has been observed in another part of East Africa. The Dinoflagellates are recorded from four lakes, and a comparison may thus be instituted. Lake Victoria contains representatives of the genera *Ceratium* and *Glenodinium**. The former genus is wanting in Tanganyika, where, however, *Peridinium* and *Peridiniopsis* replace it. In Nyasa, *Ceratium* and *Peridinium* occur; in Lake Albert, *Peridinium* and *Glenodinium*. It is particularly among the ciliated forms that a number of genera occur represented only by a single species. The *Trichodina* mentioned, which has not been specifically identified, is parasitic upon the Tanganyika jelly-fish. Since the latter, or a variety of it, is known from Victoria Nyanza, it may well be that a *Trichodina* accompanies the medusa there also, but I have no information on the subject.

In conclusion, it only remains to point out that the Protozoa, as at present known, give no indication of an exceptional fauna peculiar to any lake. At the same time it is precisely in Tanganyika, if anywhere, that such might be expected, and that lake remains virtually unexplored in this direction.

4. GENERAL DISCUSSION AND CONCLUSIONS.

Having completed the systematic review of the animals at present known to occur in the lakes, the points of interest concerning their distribution may now be fittingly discussed. Far the most noticeable feature is that which has so repeatedly shown itself, namely the unique nature of the fauna of Tanganyika. With a recorded total of over 400 different animal types, the lake is clearly exceptional; moreover, no details of certain groups which are known to occur are yet available for incorporation. As this treatise is concerned so largely with Tanganyika, it may not be out of place to illustrate here in a graphic manner, the growth of knowledge concerning its fauna.

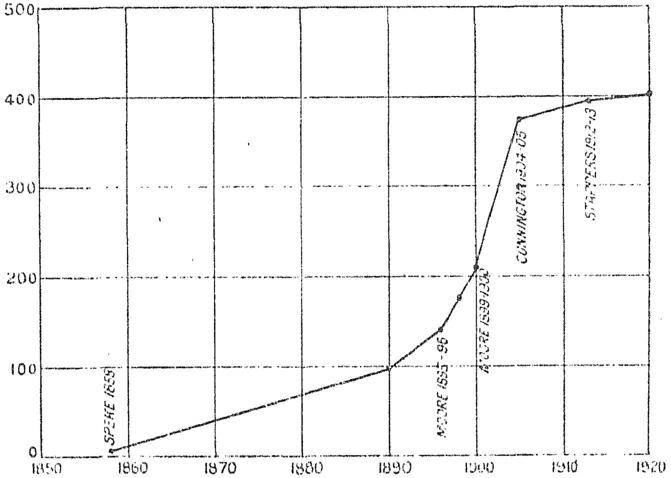
The curve which follows may be regarded as approximately correct. It is clear that the labour of ascertaining the date of discovery or description of every type—even if possible—would be out of proportion to the value of such a record. The largest addition to the total (159 species in all) was made by the writer's expedition, which obtained, moreover, practically all the information on the flora of the lake.

---

* Virieux states that in the plankton which he examined he observed a specimen of *Peridinium*, but was unable to identify the species (**197**, p. 6).

Text-figure 1.

Curve showing growth of knowledge of Tanganyika fauna.



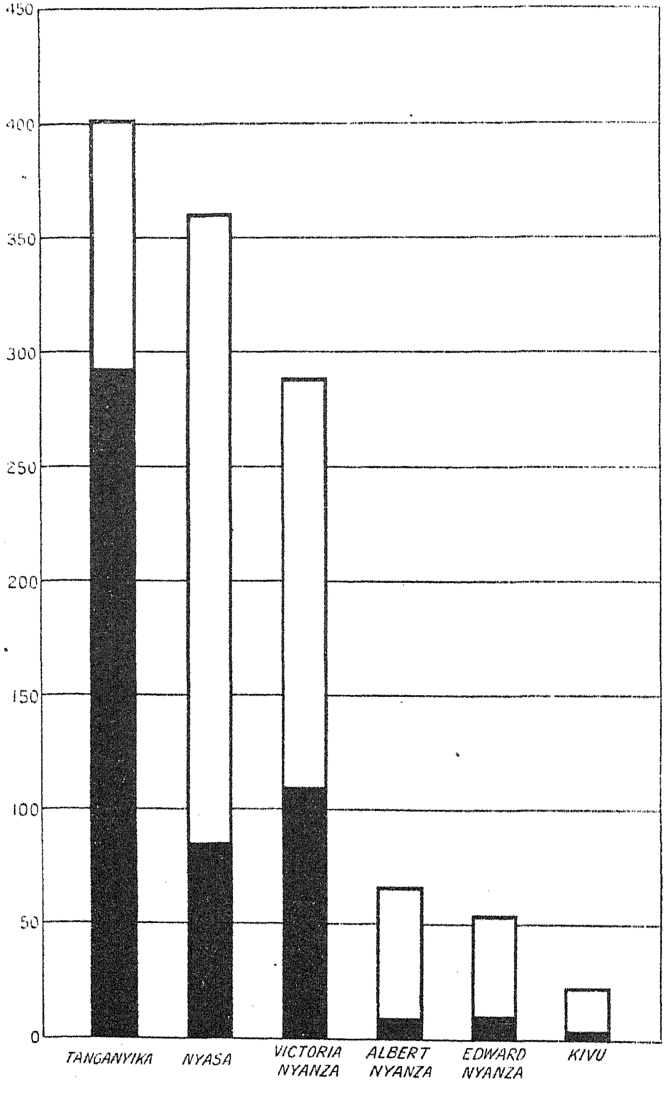
The relative peculiarity of each lake fauna, as far as totals only are concerned, can be best illustrated by giving the figures in parallel columns with the marks E or P against them.

	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Kivu.
Genera	57 E, 111 P. (168)	2 E, 137 P. (139)	6 E, 172 P. (178)	1 E, 47 P. (48)	1 E, 34 P. (35)	13 P.
Species	293 E, 109 P. (402)	110 E, 179 P. (289)	86 E, 275 P. (361)	9 E, 58 P. (67)	11 E, 43 P. (54)	4 E, 19 P. (23)

An examination of these totals at once reveals the chief points in which the fauna of Tanganyika is distinct. In the first place, the lake contains a more extensive series of forms (402) than any other. In the second place, those types greatly predominate which are unknown elsewhere (293 out of 402). Both these points, viz. total number of species and corresponding number of endemics, are shown graphically for each lake in the following table:—

Text-figure 2.

Table to illustrate richness of fauna and proportion of endemic species to the whole.



The height of each column represents the total number of species, and the shaded portion the number of endemic forms.

It will be observed that the total figure for Nyasa, though some way behind that of Tanganyika, is still very large. Since in many cases—*e. g.* fishes, molluscs, prawns—Tanganyika has a much richer fauna, such a result is perhaps a little surprising. It is worth while to recount the facts which explain this. Firstly, the group of the Cladocera is entirely absent from Tanganyika, but well represented in Nyasa and elsewhere. This is probably due to the nature of the salts dissolved in the water, which appears also to have a restrictive influence on the Rotifera of the lake. Secondly, there are one or two groups of animals—notably the Protozoa and free-living Nematoda—almost uninvestigated as far as Tanganyika is concerned, although tolerably well known for Nyasa. Lastly, the collections made by Fülleborn extended to the waters surrounding Nyasa, while the rivers, ponds, and swamps in the neighbourhood of Tanganyika remain unexplored. This has greatly increased the records for Nyasa, particularly in the groups Rotifera, Protozoa, and Entomostraca.

In the matter of endemic types, however, Tanganyika leaves Nyasa (and the other lakes) far behind, exhibiting an astonishing series of forms for which it is difficult to find a parallel. Expressing in percentages the figures already furnished, nearly 73 per cent. of the species in Tanganyika are peculiar to the lake, whilst Victoria Nyanza comes a poor second with 38 per cent., and Nyasa still further behind with some 24 per cent. The smaller lakes have not only smaller totals, but have a reduced proportion of endemic forms, namely 20 per cent. for Lake Edward, 17 per cent. for Kivu, and only 13 per cent. for Lake Albert. Nor is this all, for the number of endemic genera which Tanganyika contains places it in a category by itself. No fewer than 57 out of 168 are regarded as peculiar to the lake, or rather more than one-third of the total. As against this, Nyasa has 6 endemic genera out of 178, and Victoria Nyanza 2 out of 139, while Lakes Albert and Edward each possess but a single endemic genus. Tanganyika alone among these lakes has a family which can be regarded as endemic—that of the Tiphobiidæ (Gasteropoda).

It is thus clear that Tanganyika exhibits by far the most striking series of endemic animals of any of the lakes under consideration—indeed, it must be recognised as one of the most remarkable lakes in the world. There are only two lakes, as far as I know, which merit comparison with Tanganyika in this direction, viz. the Caspian Sea and Lake Baikal. Unfortunately I have been quite unable to obtain trustworthy figures of recent date with which to compare the particulars now available for the African lake. It seems probable, however, that Baikal even surpasses Tanganyika in the number of animal forms peculiar to its waters*. It appears that while relatively few groups are represented, there is often a great richness of species within the groups. The fishes are far fewer than those of Tanganyika and only half of them are endemic, while the Mollusca agree pretty closely in the number of endemic types. On the other hand, there are most extensive series of Oligochaetes and Turbellarians, and an extraordinary wealth of Gammarids, the species being in each case nearly all endemic. In the case of the Caspian, I am able to quote figures, according to which some 64 per cent. of the animal forms are found nowhere else in the world (**155**, p. 34). If this statement can be relied upon, the Caspian Sea, while sufficiently remarkable, is less so than Tanganyika, which has nearly 73 per cent. of endemic types.

---

* Consult the series of monographs dealing with the results of the most recent scientific expedition—Wissenschaftliche Ergebnisse einer Zoologischen Expedition nach dem Baikal-See unter Leitung des Professors Alexis Korotneff in den Jahren 1900–1902. Lieferungen 1–5. Kiew und Berlin 1905–1912. It is to be regretted that this work remains uncompleted, doubtless on account of the European war.

Returning to a consideration of the fauna of Tanganyika, other features revealed in the Systematic Account may be summarised in a few sentences. Those groups which are most conspicuous in possessing endemic genera and species are the Pisces, Mollusca (especially Gasteropoda), and Macrura, with the Brachyura following closely. The Copepoda and Ostracoda are well represented by endemic species (but not genera), with the Porifera and Polyzoa showing smaller numbers. While other groups with few endemic species, appear, by contrast, devoid of significance, there are only five of all those represented in the lake—Mammalia, Crocodilia, Chelonia, Batrachia, and Cœlenterata—which do not contain endemic types. It may be added that certain endemic forms are held to exhibit a marine aspect and have been termed thalassoid (halolimnic according to Moore). Such are many of the Gasteropod molluscs and perhaps a Polyzoon. In the same category comes the medusa, which, of course, is not confined to Tanganyika.

The exceptional character of the Tanganyika fauna having been sufficiently emphasised, an explanation of this marked peculiarity must be sought. In other words, a general consideration of what Moore called the Tanganyika "problem" must be undertaken. In order to appreciate the actual value of the purely biological evidence, it is necessary clearly to understand the relations which exist between marine and fresh-water organisms. The essential points may therefore be stated as briefly as possible *.

In the first place, while certain organisms are characteristic of the sea and others of fresh water, the distinctions which exist between marine and fresh-water forms are neither very great nor very definite. Secondly, it may be emphasised that the barriers which tend to prevent a change of medium are not wholly insurmountable. At the same time fresh-water types are usually recognised in consequence of certain structural peculiarities directly due to their mode of life. Such features should be excluded as far as possible when deciding the systematic position of an organism, for it is only thus that a true idea of its interrelationships—which are quite independent of habitat—can be obtained.

---

* These matters are discussed at greater length in several recent papers. Consult Sollas (**173**), Cunnington (**71**), Gurney (**97**).

The undoubted affinities existing between marine and fresh-water organisms are the direct result of a community of descent, for there is no escape from the conclusion that life had its origin in the ocean. Thus the forms now found in fresh-waters must have attained their present distribution in one of three ways:—(1) by a direct, active or passive migration from the sea; (2) by becoming terrestrial or swamp-loving in nature, and secondarily adapting themselves to life in fresh water; (3) as a result of the isolation and subsequent freshening of some portion of the sea, due to movements of the earth's crust. Without speculating as to which of these methods has played the most important part, it may be pointed out that the salinity of the ocean has not been constant throughout the ages, but is doubtless greater now than in past geological times. Since certain types are known to have recently migrated from the sea, it is not hard to believe that many forms may have achieved the change during former epochs when the obstacles to be surmounted were somewhat less. It is hardly necessary to repeat that the view advocated by Moore assumes that the remarkable organisms found in Tanganyika have attained their present distribution by the third means, and have been modified from marine types in a basin cut off from the sea.

Since the flora of a lake perforce exists under the same conditions as the fauna, it will be well, before proceeding, to make further reference to the plants of Tanganyika. The higher plants show no outstanding peculiarities. There are certainly 8 species of true aquatics which have been collected in Tanganyika alone among the lakes, but all these are well-known African—or even cosmopolitan—forms (*cf.* Rendle, **147**). On the other hand, the Algæ of Tanganyika differ markedly from those found in the other big lakes, a number being endemic, while a few are usually marine or brackish in habit. In all, some 21 species and 5 varieties are described as peculiar to Tanganyika. It is, however, the phytoplankton of the lakes which affords the most interesting comparisons. The plankton of Tanganyika is much richer in species than that of either Nyasa or Victoria Nyanza. Out of a total of 85 species, more than 70 per cent. do not occur in the other two lakes, so that in this instance once more the features characteristic of Tanganyika are exhibited. The presence in the lake of brackish-water and quasi-marine Algæ may perhaps be accounted for by a period of growing salinity prior to the establishment of an outlet. (For further particulars consult the detailed Report on the Fresh-water Algæ of the Third Tanganyika Expedition, **260**).

It is natural that a good deal of attention has been attracted to Tanganyika by the singular nature of its fauna, and it is not surprising that various suggestions have been offered in explanation of the facts. While it will be necessary to recount the several views which have been advanced, it is appropriate to deal in the first instance with Moore's hypothesis that Tanganyika represents an old Jurassic sea. This view, first put forward in a paper published in 1898 (**131**), was subsequently developed and the evidence detailed at considerable length in "The Tanganyika Problem," 1903, (**137**). Being thus a widely known theory, it is only necessary to inquire how it accords with the facts which have since come to light. From the botanical and geological, as well as from the zoological side, more information is available than when this hypothesis was propounded, and it may at once be said that recent discoveries do not favour the theory. As the zoological evidence has been examined and discussed in the body of this paper, it is only needful to summarise the conclusions.

Moore's view rests in the main on his comparison of certain marine fossil shells of the Jurassic period, with those of Gasteropods living in the lake at the present day - coupled with his deductions as to the anatomy and relationships of the latter forms. It has already been explained (p. 549) that, in the opinion of leading experts, neither of these claims can be substantiated. If the comparison with Jurassic fossils is held to be inadmissible, the period of the supposed connection with the ocean remains in doubt, but while Moore subsequently declared that he attached no great weight to this comparison (**138**, p. 602), he still adhered to his view that the so-called halolimnic animals were truly marine or relict forms. As far as the molluscs are concerned, the opinion of Pelseneer is in direct conflict with this view, for he regards the halolimnic Gasteropods as emphatically fresh-water types.

In this connection it may well be asked—why are there no thalassoid Lamellibranchs in Tanganyika? There seems no obvious explanation of the fact, yet surely some members of this group would also exhibit a thalassoid appearance had they been relict forms from the ocean. This itself is evidence which tells against the view of a relict origin for the fauna.

Nor do the other members of Moore's group of halolimnic animals definitely support his contention. The medusa, once so important, and admittedly a marine type, has lost most of its significance. Not only are fresh-water medusæ known to occur more widely than was formerly supposed, but the Tanganyika species has been found in the Niger and in Victoria Nyanza. The Decapod Crustacea—prawns and crabs—regarded in "The Tanganyika Problem" as constituents of the halolimnic group, have been shown to belong to typically fresh-water families. Much stress was formerly laid upon the incrusting gymnolæmatous Polyzoon *Arachnoidea*, but recent discoveries have modified its importance. Since the genus is now actually living in Asiatic seas, it can hardly be regarded as an ancient marine type persisting only in Tanganyika, but must rather be looked upon as a recent importation (*cf.* the analogous case of *Victorella*, p. 540). Finally the sponges belong to the family Spongillidæ, a characteristically fresh-water assemblage. Thus, of the succession of animals from different groups which constituted Moore's halolimnic series, none are accepted as peculiarly marine save the Polyzoon *Arachnoidea* and the medusa.

But more than this. The endemic animal forms have been described almost without exception as specialised and not primitive types. It is true that Moore regarded the remarkable Gasteropods as essentially primitive in nature, but this view is not shared by other writers (p. 550). If the halolimnic animals are indeed relict forms, they must have been cut off at some remote era—though it need not have been the Jurassic period—and ought in consequence to exhibit primitive rather than specialised characteristics.

This review of the zoological evidence makes it clear that on such grounds it is impossible to justify the contention that Tanganyika was connected with the sea in Jurassic times, or indeed that a connection with the sea ever existed. It is therefore necessary to inquire what light may be thrown on the subject by the evidence of geology.

In his book, Moore maintained that resting on the Archæan granites, gneisses, and schists which appear to constitute the basement rocks of the continent, three types of sedimentary rock are to be recognised. The lowest of these consists of beds of sandstone and shale, which are not only well developed in the neighbourhood of the great lakes, but appear to extend over vast areas of the African interior, including a large part of the Congo basin. Then follow the beds discovered by Drummond northwest of Nyasa, and covering these in turn, white shelly deposits (Pleistocene) laid down by the lakes themselves. Drummond's beds being regarded as Triassic in age and probably estuarine, Moore considered the great beds of sandstone and conglomerate as evidence of an extensive ocean which at some still earlier period covered a great part of the lake regions of Central Africa (**137**, p. 65 *et seq.*).

It is particularly to this last point that exception is taken by other writers on the geology of these regions. Some regard Drummond's beds and the great sandstone series as of like age, and on the evidence of the fossils occurring in the former, regard the whole as beds of the lower Karoo (Trias)—or at least as a formation of corresponding age, deposited under similar conditions. A very recent writer on the stratigraphy of this part of the continent (Behrend) speaks of the unfossiliferous conglomerates, quartzites, and sandstones which are particularly well displayed in the neighbourhood of the great lakes, as the "Tanganyika System" (**14**, p. 52). These beds he distinguishes as of different age from similar rocks occurring near Nyasa and in parts of the Congo basin, assigning them to an earlier period—Devonian or even prior to that (**14**, p. 73 and Taf. iii.). While it may be that the relative age of these different strata is by no means conclusively fixed, these recent investigations show that Moore's lowest series—the "Old African sandstones" as he calls them—really comprises two or more formations. In any case all the evidence goes to prove that these sandstones and conglomerates, whatever their age, were laid down under continental, *i.e.* fresh-water and terrestrial conditions, and thus afford no support for the view that the ocean formerly extended over these large tracts in the heart of Africa.

There is yet another geological objection to the view that Tanganyika contains relict forms from an ancient sea, and that is, that the depression itself would not appear to date back to the remote times required by Moore's hypothesis. There is every reason to believe that the extensive faulting which produced the Great Rift Valley took place in Middle-Tertiary times, and if this be accepted, the basin of Tanganyika was actually not in existence at the time when the Jurassic theory supposes it to have received its marine fauna *.

Clearly the geological evidence does not favour a marine "relict" origin for the peculiar fauna of Tanganyika, and it has been shown that the testimony of zoology is against it. In order to be convincing, a theory must not run counter to the findings of either branch of science.

Since it does not seem possible to accept the hypothesis put forward by Moore, alternative suggestions have now to be considered. In the first place, it is important to point out that shells of the thalassoid Tanganyika genus *Paramelania* had been compared by White (**202 : 203**) and Tausch (**186**) with those of the fresh-water Cretaceous genus *Pyrgulifera* some time before Moore drew his comparisons with marine Jurassic shells. It has been held by conchologists that the resemblance in this case is every whit as close as between any of the forms compared by Moore. This may constitute slender evidence on which to theorise, but it is significant that the beds from which the fossil type comes are not only more recent, but are fresh-water in character and not marine. Thus, if any value attaches to the evidence, it would suggest that the unusual molluscan genera should be regarded as the little modified representatives of a late secondary fresh-water assemblage rather than those of a much earlier marine one. This view, which implies that the thalassoid Gasteropods are relics of an ancient lake fauna preserved in this basin, obviously did not find acceptance by Moore. He urged against it the pertinent fact that in such a case, similar types, living or fossil, ought to be found in other areas, and yet they are conspicuously absent (**137**, p. 335). While agreeing that this constitutes a serious objection, the same objection, to my mind, may be raised with equal force against the marine Jurassic hypothesis.

Reference has already been made to the fact that certain fossil Gasteropods from the Balkan Peninsula exhibit a considerable resemblance to some of the thalassoid types from Tanganyika

---

* Certain geological experts, indeed, regard the Tanganyika basin as more recently produced than other parts of the Rift Valley system.

(p. 550). The forms in question, described and figured by Brusina (**58 : 59**), come from fresh-water Pliocene beds in Dalmatia, Croatia, and Slavonia. From this it might be argued that the lakes of the Mediterranean region which existed in Tertiary times were the source from which the Tanganyika Gasteropods have been derived. It is not unreasonable to suggest that communication was possible between these lakes and the region of Tanganyika by way of the valley of the Nile and the Great Rift Valley. While less objection can be taken to this view than to Moore's, or even to the suggestion of a Cretaceous origin for the molluscs, there are difficulties in accepting it as a complete solution of the problem. To confirm this theory, either fossil forms of like nature should be forthcoming in some intermediate region, or (as a communication to the north of Tanganyika is assumed) living types should be found in Lakes Kivu, Edward, or Albert. Since neither are known to occur, the case for this source of origin is unsupported.

Since the shells of the thalassoid molluscs have been held to resemble (1) marine Jurassic types of the Anglo-Norman basin, (2) in one instance a widely distributed fresh- or brackish-water genus from the Upper Cretaceous of Hungary and North America, (3) a series of fresh-water fossils from beds of Newer Tertiary age in Jugo-Slavia, the evidence afforded is so contradictory as to offer little guidance in determining the origin of the fauna of Tanganyika.

It is a very natural suggestion that the thalassoid appearance of the Tanganyika Gasteropods is directly due to the size, depth, and quasi-oceanic conditions prevailing in such a lake *. That is to say, that a marine aspect has been produced in certain members of the ordinary African fresh-water series as the result of convergence. To those who have visited these lakes and realised their vastness this seems plausible, but the difficulty has then to be faced, that similar forms are not forthcoming in Nyasa and Victoria Nyanza.

An hypothesis in which this view is introduced, but which has other novel features, was brought before the International Congress of Zoology in 1913 by Germain (**87**). He holds that previous writers have been wrong in considering Tanganyika by itself, and urges that a clearer understanding of the facts becomes possible on taking into account the organisms which inhabit neighbouring lakes and rivers. Dealing with the Prosobranch Gasteropods, which exhibit *par excellence* a thalassoid facies, Germain asserts that while Tanganyika contains a much larger series of such forms than any other lake, it is not the sole locality in which they may be found. He considers that Lakes Mwero and Nyasa, as well as the Upper and Middle Congo, contain a number of Prosobranchs (chiefly Melaniidæ) the marine aspect of which it is impossible to deny. Proceeding to discuss the geological aspect of the problem, he states that very extensive lacustrine deposits are actually known in Central Africa, reaching from the Congo basin to Tanganyika and from that lake to Victoria Nyanza on the one hand and Nyasa on the other. From such considerations he supposes that there formerly existed in east-central Africa a vast lake basin which united the Middle and Upper Congo with Nyasa and Tanganyika and probably Victoria Nyanza. Living in this region was a uniform fresh-water fauna specially rich in Prosobranchs. After the formation of the Great Rift Valley the lakes were isolated in their present basins, where modifications of the original fauna resulted from the new environment. Lake Tanganyika, possessing most nearly the characteristics of the ocean, became inhabited by molluscs which have assumed (by a phenomenom of convergence) a marine aspect in the highest degree*.

---

* A corresponding suggestion has been made to explain the marine appearance of certain Crustacea and other organisms in Lake Baikal.

With this conception I do not find myself wholly in accord. Without expressing an opinion on the nature of the Gasteropods of Nyasa and the Upper Congo region, there are two serious objections to its acceptance. In the first place, there is insufficient geological evidence for a lake basin so large in extent the deposits in this area being probably terrestrial and fluviatile. In the second place, there is no reason why the conditions in Nyasa and Victoria Nyanza, which closely resemble those of Tanganyika, should not have produced an equally striking series of thalassoid Gasteropods in those lakes, and yet this is not the case. At the same time I am quite prepared to agree that the marine aspect of the molluscs is probably due to convergence.

Another obvious suggestion is that the salinity of the water has been a determining factor in producing marine-like forms. Here it is much less easy to come to a decision, for the question of increased salinity is of course directly associated with that of a period of isolation. But prolonged isolation itself, with the opportunity it affords of development free from competition with the outside world, is obviously a cause predisposing to the production of new characters. Where isolation and a gradual increase in salinity have coexisted, it is difficult to recognise which factor is responsible for a particular result. Experimental evidence is not wanting to show that certain salts, even in minute quantities, exert a profound influence on aquatic organisms, but it does not follow that a marine aspect would be produced as a result. West, indeed, goes so far as to assert that the Algæ of Tanganyika which exhibit marine affinities may well have been produced by a gradual increase in the salinity of the lake during an extended period of time (**200**, p. 191). Here, it is true, the two factors are inextricably associated, but if the suggestion is not unreasonable for the Algæ, the surmise may be hazarded that the thalassoid Gasteropod shells owe their nature to the same cause. Be this as it may, there are additional complications affecting the salinity of Tanganyika.

---

* Since this account has been in the press, a still more recent paper by Germain has reached my hands—"Histoire Océanographique des Lacs de l'Afrique Orientale." Bull. Inst. Océanogr. Monaco, No. 369, 1920. In it, he adds little which is new, merely re-affirming the opinions expressed in his earlier article.

It has been shown that Tanganyika had probably no outlet until a portion of the Nile basin became cut off and Kivu drained south into the lake (p. 515). It has also been pointed out that since Kivu water contains an excessive amount of magnesium salts, that lake is probably the source from which the high percentage in Tanganyika has been derived (p. 570). If these probabilities be accepted, certain conclusions as to salinity follow. During the first period the salinity may well have been considerable, though there is no evidence as to its nature. The lake subsequently freshened, but eventually its waters became rich in salts of magnesium. Thus any effect which the saline nature of the water may have exerted on the organisms of the lake may have been due to either of these conditions, or to a combination of both. As already suggested, there may even exist an irregularity in the outflow of the lake, due to the forming and breaking of dams in the bed of the Lukuga River (p. 515). If this be the case, the salinity of Tanganyika has not only changed considerably in the past, but may still be changing materially from time to time.

The view that Tanganyika owes its remarkable organisms— not merely the thalassoid forms—to a long-protracted period of isolation, has been advocated by several writers, and remains, on the whole, the most likely suggestion put forward. The possible effect of an increased salinity, which isolation would involve, must of necessity be coupled with this, but it is not regarded as the prime factor. This view has the positive advantage that it does not run counter to geological conceptions, but fits in with what is believed to be the past history of the lake.

Testimony in favour of it is afforded by the very remarkable nature of the Cichlid fishes which Tanganyika contains. This group has long been known to show a peculiar facility for colonising isolated and often saline waters, though the agency by which this is effected is not understood. What then more likely than that the Cichlids were among the earliest inhabitants of the lake, where, without having to compete with other types of fish, they multiplied unchecked and became differentiated into new genera and species (*cf.* **26**, p. 423).

It is hardly necessary to point out that this isolation hypothesis does not assume that Tanganyika was stocked from any exceptional source. That is to say, the lake did not receive its fauna from an ancient sea, but in the same manner as the neighbouring fresh-waters, the original similarity of its fauna to those of the other lakes being secondarily lost by marked divergences of form consequent upon prolonged isolation. The marine aspect of certain Gasteropods would thus be regarded as merely due to convergence. Viewed in this light, the case of Tanganyika is closely analogous to that of oceanic islands, which, as isolated areas of land, are well known to possess faunas and floras largely peculiar to themselves.

The last-mentioned hypothesis, even if satisfactory in the main, makes no attempt to account for the presence of the medusa in Tanganyika, and accordingly a few sentences are needed on this aspect of the question.

In dealing with the distribution of African fresh-water fishes, Boulenger has discussed the problem of Tanganyika, and states that he cannot admit Moore's contentions (**26**, p. 422). He refers to the inconclusive evidence afforded by the so-called halolimnic Gasteropods, and clearly regards the medusa (now known from other parts of the continent) as the only organism in the lake for which it is necessary to account in any special manner. He points out that palæontological evidence exists of a Middle Eocene (Lutetian) sea which extended over a large area in Northern Africa (*vide* also Hudleston **102**, p. 352), and suggests that this would afford a rational explanation of the present distribution of the medusa in Africa.

With this view Gravier is not in agreement (**90**, p. 221). He gives it as his opinion that the medusa may well have migrated from the sea at a recent epoch, especially should it possess a hydroid stage, as is held likely by Browne (*cf.* **56**, p. 306). Its present distribution in Africa he explains by reference to the possibilities of intercommunication between the river systems.

Having dealt at considerable length—as becomes its importance—with the fauna of Tanganyika and the views put forward to account for its very unusual character, it is now possible to proceed to a brief study of the remaining lake faunas. While there are smaller totals and fewer peculiar types, the bigger lakes at least are not devoid of interest.

Victoria Nyanza, with 38 per cent. of endemic species, clearly has characteristics of its own, these being more prominent in some groups than in others. By far the most conspicuous group is the Pisces, containing, as in the case of Tanganyika, the largest series of forms. It comprises also over half the total number of endemic species and the only two endemic genera. The Mollusca again are noteworthy, but in this case the Lamellibranchs are more striking than the Gasteropods, exhibiting a larger proportion of endemic types. Of the few Ostracods recorded from the lake, 5 out of 7 are described as peculiar, and the Oligochæte worms are represented by 6 species, 4 of which are endemic. Victoria is the only lake besides Tanganyika which contains the medusa, though this should perhaps be regarded as subspecifically distinct. It is only in this lake that the common *Hydra* is known to occur. Many groups are wholly without endemic representatives.

Generally speaking, Lake Nyasa exhibits very similar features, but with rather fewer peculiar forms. Fishes constitute half the total number of endemics, and 5 endemic genera out of 6. A considerable number of molluscs are known, nearly half being peculiar to the lake. Nyasa contains an endemic genus belonging to the Argulidæ, and the Ostracoda are well represented, 8 species being endemic out of 17. It is strange that no aquatic snakes and no Polyzoa have yet been recorded; on the other hand, Nyasa alone of the lakes under review contains aquatic tortoises referred to the Trionychidæ.

The three smaller lakes contain representatives of fewer animal groups, but it is possible that this is merely due to less systematic investigation.—Albert Nyanza displays only 13 per cent. of endemic forms, which are mostly Mollusca, while it has no endemic fish. The genus *Limnocaridella* (prawn) is the only genus peculiar to the lake.—Edward Nyanza contains a more interesting series of fish, with one genus and six species endemic. Only 3 molluscs are peculiar out of a total of 15, and there is little else which calls for comment.—In Kivu, representatives of only 6 groups of animals are at present known to occur. While future exploration may bring other forms to light, the poverty of its fauna is probably connected with the exceptional salinity of the water. Out of a total of 23 species, there are 13 fishes, 3 being endemic, while the only other endemic type is an Oligochæte worm. The apparent absence of the hippopotamus and the crocodile is a point of some interest. Similarly no Lamellibranchs appear to occur, although two forms of Gasteropod are known.

It is obvious that none of these lakes exhibit such striking forms as Tanganyika, and that while endemic types are not wanting, these are fewer in number and for the most part only specific in character. Apart from the presence of the medusa in Lake Victoria, there is nothing to suggest a special connection with the sea. In broad terms it may be said that the lakes contain the ordinary fresh-water fauna of Africa modified in varying degree in each case. Where such modification is considerable, as in Victoria Nyanza and less markedly Nyasa, it may well have been caused by a period of isolation proportional to the relative peculiarity of the fauna. It is more especially the fish-fauna of these lakes which is rich in endemic species and shows certain endemic genera, and from this evidence it would seem that Lake Victoria remained isolated for a longer period than Nyasa (*cf.* p. 536). If isolation be accepted as accounting for the remarkable fauna of Tanganyika, it is clear that a still longer period must have been necessary in that case to produce such notable results.

There are certain other matters concerning the distribution of animals in the African lakes which are brought out by this comparative survey. While representatives occur of most of those groups which may be expected in tropical fresh waters, there are some interesting exceptions. It comes as a surprise to a European naturalist to find no fresh-water Isopods such as *Asellus*, or Amphipods such as *Gammarus*, yet these familiar forms appear to be conspicuously absent from the tropical parts of Africa, though the genus *Gammarus* is recorded from the north and south of the continent. Why such types are wanting it would be idle to speculate, but the fact is also emphasised by Stuhlmann in more than one place (**181**, p. 1268 : **182**, p. 652). It is strange too, that among the intestinal parasites of the fresh-water fish there appear to be no species of *Echinorhynchus*, although they are common in the fish of European rivers. Daday, it is true, has described a larval form from a species of Ostracod taken in a small East African lake (**76**, p. 55). Thus, while *Asellus* and *Gammarus* are commonly the intermediate hosts, it is evident that the absence of these genera does not form a complete barrier to the distribution of *Echinorhynchus*, and Daday considers that it will yet prove common in Africa. At present, however, the adult form is entirely unknown.

Concerning the numerical distribution of species in the lakes, there is one point which calls for further notice. From a study of the lists of forms found in each lake, Moore believed that a definite relation existed between numbers and size. After reviewing the facts then at his disposal, he writes : —"It is thus obvious that from some cause or other the number of specific forms in an African lake is roughly proportional to the size of the lake itself" (**137**, p. 146). This does not mean that the smaller lakes are less well stocked with animals, but simply that the number of species they contain is less. The matter has already been referred to in the systematic section, and it has moreover been shown that the principle appears capable of extension to the number of genera and even families (pp. 535, 548). With the total figures for the six lakes now available, it is possible to test the correctness of this conception on a more extended basis. The totals for species and genera are therefore given in tabular form, with the lakes (apart from Tanganyika) arranged in order of size.

	Tanganyika.	Victoria Nyanza.	Nyasa.	Albert Nyanza.	Edward Nyanza.	Kivu.
Number of Species	402	289	361	67	54	23
" Genera	168	139	178	48	35	13

Tanganyika, which heads the list, is in every sense to be regarded as a case apart, but the figures for the remaining lakes should accord with this law—if such it be. A descending series is seen to exist : Nyasa it is true constitutes an exception, but, as already explained, its totals have been artificially swollen in certain directions (p. 595). Nyasa conforms to the rule in the case of the Pisces and Mollusca—it is the addition of many types of Rotifera and Protozoa which chiefly accounts for the large total figure for the lake.

A very similar result is arrived at on comparing the number of groups represented in the different lakes. From Victoria Nyanza downwards the decrease in size is accompanied by a decrease in the number of groups present. The figures (including Tanganyika for comparison) are found to be as follows:—Tanganyika 26 (groups), Victoria 25, Nyasa 24, Albert 15, Edward 14, and Kivu 6. It is possible, however, that the low totals for the smaller lakes are, in part, a result of less complete investigation.

Enough has been said to show that Moore's contention is substantially correct as far as these African lakes are concerned. It would be interesting to discover whether a similar relation between size and number of specific forms can be made out for other groups of lakes or even if it is a principle of general application. Moore makes a comparison, which would seem to be justified, between this phenomenon and that exhibited by the flora of oceanic islands, where the smaller the island,—although it may be as thickly covered with vegetation as any other area,—the fewer the species of plants which inhabit it.

The last matter to be considered is the undoubted affinity which exists between certain African and Indian fresh-water types—an affinity which has been noticed already, when reviewing the groups in which it is most pronounced. This inter-relationship is exhibited in many groups of animals, and extends not merely to forms from the Indian Peninsula itself, but from the whole of that part of Asia, including the Malay Archipelago. An interesting account of these affinities is given by Annandale in a paper entitled "The African Element in the Freshwater Fauna of British India" (**10**). So far as the present treatise is concerned, consideration is limited to those animals which are known to occur in one or other of the big African lakes. Briefly enumerating the cases, the Cyprinidæ and Mastacembelidæ among the fishes indicate this affinity in a marked degree. The Polyzoa afford striking evidence, since the genus *Arachnoidea* is known from Tanganyika and East Indian seas, while in the case of *Plumatella* (*Afrindella*) *tanganyikæ* the actual species has been found in an Indian lake as well as in Tanganyika. *Caridina nilotica* with its varietal forms occurs in several of the African lakes, while it is widely distributed in Indian and Malay regions and extends still further east into Australia. Among the Cœlenterata a medusa has now been found in India which is generically identical with that from Tanganyika and Victoria Nyanza, while finally among the sponges *Spongilla carteri* from Lake Victoria is known in India and Java.

This is not the place to discuss the geological evidence for a former land-connection between these areas, but the views commonly held can be stated in a few words. During the Carboniferous period, and persisting subsequently through the Permian and Triassic, there appears to have existed a vast tropical continent which extended from Brazil to Australia, embracing of course Africa and India. This continent is known as Gondwanaland. In the ensuing period—the Jurassic—Gondwanaland began to break up, but there is some evidence that in late Cretaceous or even early Tertiary times a land-bridge still existed between East Africa and the Indo-Malayan region, by way of the Seychelles and Maldives. The geological record is thus quite in keeping with the facts of distribution to which reference has been made.

In bringing this study to a conclusion, it must be admitted that in many directions information is very limited. There is no doubt that the discovery of additional species is to be expected whenever a re-examination of any of the lakes occurs, but there are other points of considerable interest on which knowledge is much to be desired.

Despite the investigations of Moore in Nyasa and Tanganyika, very little is really known concerning the deeper regions of any of the lakes, and the existence of a distinct abyssal fauna is uncertain. In a paper dealing with the distribution of the molluscs, Moore speaks of obtaining certain thalassoid forms in Tanganyika at a depth of 800–1200 feet (244–366 metres) (**129**, p. 171). He regarded these particular Gasteropods as a deep-water assemblage, but a more thorough examination may well reveal other animals which permanently inhabit the bottom muds. There is little doubt from an analogy with other deep lakes that the deeper waters of these African lakes are almost, if not quite, devoid of life. At the same time, further investigation may indicate a definite association of abyssal forms not only in Tanganyika, but in the other lakes under review.—Associated likewise with the distribution of organisms within the limits of the lakes are questions such as the vertical distribution of plankton forms, as ascertained by tow-nettings. During the Third Tanganyika Expedition my operations were practically confined to surface tow-nettings, but special tow-nets worked from suitable craft would afford the necessary information. Again, the seasonal variations of plankton organisms are almost unknown, although I was able to detect a marked decrease in the quantity of material during the rainy season. Detailed knowledge of this kind can only be gained by the aid of large collections extending over many months.—The distribution of local forms or varieties within the limits of a single lake was discussed by Moore in his book. He considered that certain well-marked varieties or even species were confined to particular areas in the greater African lakes (**137**, p. 149). My own observations lead to a different conclusion, and the matter undoubtedly merits further investigation.

Lastly, there are some outstanding physical matters which are of importance on account of their relation to biological phenomena. Very little is known concerning the chemical impurities of the water in these lakes, and even the depth and general nature of the basin is imperfectly known save for Tanganyika, Victoria and Nyasa. Further knowledge is likewise desirable as to water temperatures, seiches, and the possible occurrence of temperature seiches.

It is clear, nevertheless, that from the facts already established, a reasonably true conception may be formed both as to the nature of the lakes themselves and that of the organisms which they contain. It has been the aim of this work to supply a connected account of these facts, based on the most recent particulars. Considering the difficulties which beset the investigator in a tropical climate far from civilisation, the amount of information available is not discreditable to those concerned.

5. SUMMARY.

The special interest attaching to this comparative study of African lakes is due to the remarkable nature of the fauna of Tanganyika. That lake was discovered in 1858 by Burton and Speke, the latter bringing back with him shells considered to have a distinctly marine appearance. Subsequent collections emphasised this point, and interest was further increased by the discovery of a medusa by Böhm. A scientific expedition to investigate the fauna was despatched in 1895 in charge of J. E. S. Moore. The rich and unusual nature of the fauna then collected led him to formulate the hypothesis that Tanganyika represents an old Jurassic sea. In order to test the validity of this hypothesis, a second expedition, on which Moore was accompanied by Fergusson, left England in 1899. The result was held by Moore to justify the theory, and he embodied his conclusions in a work entitled "The Tanganyika Problem," published in 1903. As the aquatic flora had not been taken into account, a third expedition was despatched to rectify that omission and make a further collection of animals. This left in 1904 in charge of the writer, returning in 1905. More recently still, in 1912–13, the Belgian expedition of Louis Stappers visited the lake and obtained additional information.

The scope of this paper includes, besides Tanganyika, the five adjacent lakes of most interest, viz.:—Victoria Nyanza, Nyasa, Albert Nyanza, Edward Nyanza, and Kivu. All these, with the exception of Lake Victoria, occupy portions of the Great Rift Valley, which has probably been formed by trough-faulting on a stupendous scale. They lie in long narrow depressions bounded by escarpments rising to a height of two or three thousand feet above the level of the water. Nyasa and Tanganyika are very deep, the former reaching to over 780 metres and the latter to no less than 1435 metres. Victoria Nyanza has the largest area, but occupies only a shallow basin bounded by low hills.

In all the lakes, but especially the largest, conditions are almost oceanic. Climatic differences are negligible, but water temperatures are uniformly high, showing an average of about 26° C. Analyses of the water have been made in very few instances. The water of Tanganyika, while fresh, is unusually rich in salts of magnesium, and that of Kivu contains excessive quantities of the latter as well as sodium salts. It is likely that the salinity of Tanganyika was greater formerly, and may still be subject to variation. Evidence exists of a considerable rise and fall in the level of the lake, yet it seems probable that rainfall and evaporation are very nearly balanced. There is reason to believe that Tanganyika had no outlet until it received an additional water supply from the Kivu basin, which was cut off from the Nile, and added to the drainage area of the big lake by the formation of a volcanic dam in recent geological times. Tanganyika would thus have been completely isolated and its waters more saline until an outflow was established. The present effluent appears to have been formed as an affluent, its bed being finally captured by a tributary of the Congo. A periodic rise and fall in the lake level may be caused by a temporary damming of the bed of the effluent, indirectly due to irregularities in the rainfall.

As regards fauna, it is probable that at the present time all the six lakes have received fairly equal investigation. Only strictly aquatic animals are considered in this paper, but forms obtained from the neighbourhood of a lake are included in the totals. Tanganyika exhibits by far the most remarkable features, containing some 402 species of which 293 (nearly 73 per cent.) are endemic. Nyasa has a total second in point of size, but this has been artificially swollen by extra-lacustrine records which are wanting for other lakes. It has only 24 per cent. of endemic forms, while Victoria Nyanza with a smaller total has a larger percentage of endemics, namely 38 per cent. The three smaller lakes show a great reduction both in number of types and number of endemics. Tanganyika is further distinguished in that 57 out of 168 genera are peculiar to its waters, whereas Nyasa can only muster 6 endemic genera and the other lakes fewer still.

The fishes of Tanganyika are of outstanding interest, comprising 146 species, of which 121 are endemic. The most notable feature is the number and high degree of specialisation of the Cichlidæ, which with 27 genera (21 endemic) and 89 species (84 endemic) is the richest Cichlid fauna in the world. A species of incrusting gymnolæmatous Polyzoon occurs, such forms being mostly marine. There is a large molluscan fauna, and of the Gasteropods more than two-thirds exhibit a marine-like appearance. These are known as the thalassoid or halolimnic group and are without exception endemic. There are no thalassoid Lamellibranchs. Twelve species of prawns are known, typically fresh-water in character, but specialised and all peculiar to the lake. There is an endemic genus of crabs, with 3 species. The Eucopepoda, Branchiura, and Ostracoda are well represented, each showing a large proportion of endemic species. The Cladocera are conspicuously absent from the lake and the Rotifera are relatively few in number. This may be related to the salinity of the water. The medusa originally described from Tanganyika has now been discovered in Victoria Nyanza and the Niger. There are four endemic species of fresh-water sponges. Only 5 groups of animals contain no endemic types.

Tanganyika is one of the most remarkable lakes in the world, the only cases comparable being the Caspian Sea and Lake Baikal. Recent figures are difficult to ascertain, but while Baikal may even surpass Tanganyika in the number of unique animal forms, it appears that the Caspian is less striking.

There is reason to believe that the relations between marine and fresh-water organisms are intimate and due to a community of descent. The barriers which prevent a change of medium are not insurmountable. Organisms originated in the ocean, and have attained their distribution in fresh water in various ways. Moore regarded many of the Tanganyika types as relicts from a former ocean.

The aquatic plants of Tanganyika are of less interest than the animals. The higher plants show no peculiarities, but the Algæ differ from those of the remaining lakes. A number of species are endemic and others are usually marine or brackish in habit. The phytoplankton is rich in species, and more than 70 per cent. of the forms do not occur in Nyasa or Victoria.

Recent discoveries do not favour Moore's hypothesis of a marine Jurassic origin for Tanganyika. Neither his comparison of shells from the lake with marine fossil shells, nor his views on the primitive nature of the halolimnic Gasteropods, have been accepted by leading experts. No members of his halolimnic group, save the Polyzoon and the medusa, can be regarded as peculiarly marine. The Polyzoon is allied to a species still living in Indian seas and the medusa is known from other parts of Africa. The endemic animal types are held to be specialised rather than primitive in nature. Geological evidence is not more favourable. The extensive beds of sandstone and conglomerate which occur in the lake regions were probably formed under fresh-water and terrestrial conditions. They are considered by some to be of Triassic age, but may belong to a much earlier period, *i.e.* Devonian. Thus there is no support for the view that the ocean at one time extended over the Congo basin. Further, there is much to show that the trough in which Tanganyika lies was not formed until Middle Tertiary times.

A comparison has been made between thalassoid shells from Tanganyika and a fresh-water Cretaceous genus on the one hand and fresh-water Pliocene shells on the other. Since the thalassoid shells have been held to resemble types from such different sources, they offer little indication as to the origin of the lake fauna.—The quasi-oceanic conditions in Tanganyika may have produced an effect on the organisms it contains. Germain asserts that Gasteropods of marine aspect occur in other regions besides Tanganyika, and are derived from the fresh-water types of a former vast lake basin. On the present lakes becoming isolated, the conditions in Tanganyika produced a more striking series of such forms than elsewhere. This view is not regarded as acceptable.—It has been suggested that the salinity of the Tanganyika water has produced marine-like forms, but further evidence is needed.—The view that Tanganyika owes its remarkable organisms to a prolonged period of isolation is regarded as the most likely suggestion. It does not run counter to geological conceptions.

This theory does not account for the medusa. Boulenger suggests that it may have survived from an Eocene sea in Northern Africa. Gravier considers, on the contrary, that it may be a recent migrant from the ocean.

The faunas of the remaining lakes are of less interest. Victoria Nyanza is next in importance to Tanganyika. The most conspicuous group is the fishes, with a large proportion of endemic species. The Mollusca also are noteworthy. The fauna of Nyasa is similar in character, but with fewer peculiar types. There are, however, 5 endemic genera of fishes. The smaller lakes contain representatives of fewer animal groups as well as fewer species. Kivu is the extreme case, with only 23 species, of which 4 are endemic. The poverty of its fauna may be associated with its exceptional salinity. Albert Nyanza displays the smallest proportion of endemic types, viz. 13 per cent. It is suggested that periods of isolation would account for the peculiarities of Victoria Nyanza and Nyasa.

Certain animal types are unexpectedly absent from the African lakes. Such are the fresh-water Crustacea *Asellus* and *Gammarus* and the fish parasite *Echinorhynchus*. No explanation of this is forthcoming.

The number of specific forms in these lakes appears to be proportional to the size. This would seem to hold good also for the number of genera and families and even for the number of groups represented. It is possible that this principle is of general application. It is thought to be analogous to the phenomenon exhibited by the flora of oceanic islands.

The affinity between African and Indian fresh-water types is recognisable in several instances among the inhabitants of the lakes. This affinity is explained by the former existence of a continent which embraced these countries in the Carboniferous and subsequent periods.

Little is known of the deeper regions of any of the lakes. It remains to be discovered whether associations of abyssal animals exist in them. Neither the vertical distribution of plankton forms, nor their seasonal variations have yet been studied. Further information is needed on the salts dissolved in the water, the depth and nature of the lake basins, water temperatures, etc. It is nevertheless possible from established facts to form a true conception of the nature of the lakes and their organisms.

Bibliography.

[A number of references which are not cited in the body of this paper are included in the Bibliography in order to add to its general value. All the more important works on Tanganyika and its fauna are included, as well as the principal sources of information on the fauna of the other lakes.]

1. Adams, H. —"List of the Shells collected by Samuel White Baker, Esq., during his recent Explorations in Central Africa." Proc. Zool. Soc. 1866, p. 375.

2. Ancey, C. F. —"Résultat des recherches malacologiques de Mgr. Lechaptois sur les bords du lac Nyassa et de la rivière Shiré." Mém. Soc. Zool. France, T. vii. 1894, p. 217.

3. " "Sur quelques espèces de mollusques et sur un genre nouveau du lac Tanganika." Bull. Soc. Zool. France, T. xix. 1894, p. 28.

4. Annandale, N. —"Three Indian Phylactolæmata." Rec. Ind. Mus. vol. ii. 1908–09, p. 169.

5. " "Freshwater Sponges, Hydroids, and Polyzoa." The Fauna of British India. London, 1911.

6. " "The Occurrence of a Freshwater Medusa (*Limnocnida*) in Indian Streams." Nature, vol. lxxxvii. 1911, p. 144.

7. " "Systematic Notes on the Ctenostomatous Polyzoa of Fresh Water." Rec. Ind. Mus. vol. vi. 1911, p. 193.

8. " "Observations on the Invertebrate Fauna of the Kumaon Lakes, with special reference to the Sponges and Polyzoa." Rec. Ind. Mus. vol. vii. 1912, p. 129.

9. " "Preliminary Description of a Freshwater Medusa from the Bombay Presidency." Rec. Ind. Mus. vol. vii. 1912, p. 253.

10. " "The African Element in the Freshwater Fauna of British India." IX^e Congrès Internat. Zool. Monaco, 1913, p. 579.

11. Arnold, G., and Boulenger, C. L.—"On a Freshwater Medusa from the Limpopo River System, with a Note on a parasitic Infusorian." Proc. Zool. Soc. 1915, p. 71.

12. Beddard, F. E. —"Zoological Results of the Third Tanganyika Expedition, conducted by Dr. W. A. Cunnington, 1904–1905.—Report on the Oligochæta." Proc. Zool. Soc. 1906, vol. i. p. 206.

13. " "The Oligochætous Fauna of Lake Birket el Qurur and Lake Nyassa." Nature, vol. lxxvii. 1908, p. 608.

14. Behrend, F. —"Die Stratigraphie des östlichen Zentralafrika unter Berücksichtigung der Beziehungen zu Südafrika." Beitr. zur geol. Erforschung d. Deutsch. Schutzgebiete, Heft 15, Berlin 1918.

15. Blanchard, R. —"Hirudineen Ost-Afrikas." Deutsch-Ost-Afrika, Bd. iv. Berlin, 1898.

16. Bockelmann, A. von.—"Versuch einer Monographie des Kiwu-Sees und seiner Umgebung als Begleittext zu Dr. Kandts Karte." Beitr. Kolonialpolitik u. Kolonialwirtschaft, Jahrg. 3, 1901–1902, p. 357.

17. Böhmig, L. —"Die Turbellarien Ost-Afrikas." Deutsch-Ost-Afrika, Bd. iv. Berlin, 1898.

18. Boulenger, C. L. —"On a Freshwater Medusa from Rhodesia." Quart. Journ. Micr. Sci. vol. lvii. 1912, p. 427.

19. BOULENGER, G. A. —“Catalogue of the Chelonians, Rhynchocephalians, and Crocodiles in the British Museum.” London, 1889.

20. „ “Report on the Collection of Fishes made by Mr. J. E. S. Moore in Lake Tanganyika during his expedition, 1895–96.” Trans. Zool. Soc. vol. xv. 1898, p. 1.

21. „ “Second Contribution to the Ichthyology of Lake Tanganyika.—On the Fishes obtained by the Congo Free State Expedition under Lieut. Lemaire in 1898.” Trans. Zool. Soc. vol. xv. 1899, p. 87.

22. „ “Diagnoses of new Fishes discovered by Mr. J. E. S. Moore in Lake Tanganyika.” Ann. & Mag. Nat. Hist. 7th ser. vol. vi. 1900, p. 478.

23. „ “Diagnoses of new Fishes discovered by Mr. J. E. S. Moore in Lakes Tanganyika and Kivu.” Ann. & Mag. Nat. Hist. 7th ser. vol. vii. 1901, p. 1.

24. „ “Third Contribution to the Ichthyology of Lake Tanganyika.—Report on the Collection of Fishes made by Mr. J. E. S. Moore in Lakes Tanganyika and Kivu during his second expedition, 1899–1900.” Trans. Zool. Soc. vol. xvi. 1901, p. 137.

25. „ “Les poissons du bassin du Congo.” Bruxelles, 1901.

26. „ “The Distribution of African Fresh-water Fishes.” Report British Association, 1905, p. 412.

27. „ “On a Collection of Batrachians and Reptiles made in South Africa by Mr. C. H. B. Grant, and presented to the British Museum by Mr. C. D. Rudd.” Proc. Zool. Soc. 1905, vol. ii. p. 248.

28. „ “Fourth Contribution to the Ichthyology of Lake Tanganyika.—Report on the Collection of Fishes made by Dr. W. A. Cunnington during the Third Tanganyika Expedition, 1904–1905.” Trans. Zool. Soc. vol. xvii. 1906, p. 537.

29. „ “On a small Collection of Reptiles, Batrachians, and Fishes made by Dr. E. Bayon in Uganda.” Ann. Mus. Genova, ser. 3, vol. iv. 1908, p. 5.

30. „ “Diagnoses of new Fishes discovered by Capt. E. L. Rhoades in Lake Nyassa.” Ann. & Mag. Nat. Hist. 8th ser. vol. ii. 1908, p. 238.

31. „ “On a Third Collection of Fishes made by Dr. E. Bayon in Uganda, 1909–1910.” Ann. Mus. Genova, ser. iii. vol. v. 1911, p. 64.

32. „ “Mission Stappers au Tanganyika-Moero. Diagnoses de Poissons Nouveaux.—I. Acanthoptérygiens, Opisthomes, Cyprinodontes.” Rev. Zool. Africaine, vol. iii. 1914, p. 442.

33. „ “Mission Stappers au Tanganyika-Moero. Diagnoses de Poissons Nouveaux.—II. Mormyrides, Kneriides, Characinides, Cyprinides, Silurides.” Rev. Zool. Africaine, vol. iv. 1915, p. 162.

34. „ “A List of the Snakes of the Belgian and Portuguese Congo, Northern Rhodesia, and Angola.” Proc. Zool. Soc. 1915, p. 193.

35. „ “A List of the Snakes of East Africa, North of the Zambesi and South of the Soudan and Somaliland, and of Nyassaland.” Proc. Zool. Soc. 1915, p. 611.

36. „ “Catalogue of the Fresh-water Fishes of Africa in the British Museum.” Vols. i.–iv. London, 1909–1916.

37. Boulenger, G. A.—"Descriptions of new Fishes from Lake Tanganyika, forming part of the Collection made by the late Dr. L. Stappers for the Belgian Government." Ann. & Mag. Nat. Hist. 8th ser. vol. xx. 1917, p. 363.

38. ,, "L'évolution est-elle réversible? Considérations au sujet de certains Poissons." Comptes Rendus Acad. Sci. Paris, T. clxviii. 1919, p. 41.

39. ,, "On a Collection of Fishes from Lake Tanganyika, with Descriptions of three new Species." Proc. Zool. Soc. 1919, p. 17.

40. Bourguignat, J. R.—"Mollusques fluviatiles du Nyanza Oukéréwé (Victoria-Nyanza), suivis d'une note sur les genres Cameronia et Burtonia du Tanganika." Paris, 1883.

41. ,, "Monographie d'un nouveau genre d'acéphale du lac Tanganika." Bull. Soc. Mal. France, T. ii. 1885, p. 1.

42. ,, "Notice prodromique sur les Mollusques terrestres et fluviatiles recueillis par M. Victor Giraud dans la région méridionale du lac Tanganika." Paris, 1885.

43. ,, "Espèces nouvelles et genres nouveaux découverts par les Rév. Pères Missionnaires dans les grands lacs Africains Oukéréwé et Tanganika." Paris, 1885.

44. ,, "Nouveautés Malacologiques.—I. Unionidæ et Iridinidæ du Lac Tanganika." Paris, 1886.

45. ,, "Des Tiphobies du lac Tanganika." Bull. Soc. Mal. France, T. iii. 1886, p. 141.

46. ,, "Mollusques nouveaux de la région du Nyanza-Oukéréwé." Bull. Soc. Mal. France, T. iv. 1887, p. 267.

47. ,, "Iconographie Malacologique des animaux Mollusques fluviatile du lac Tanganika." Corbeil, 1888.

48. ,, "Mélanidées du lac Nyassa, suivies d'un aperçu comparatif sur la faune malacologique de ce lac avec celle du grand lac Tanganika." Bull. Soc. Mal. France, T. vi. 1889, p. 1.

49. ,, "Histoire Malacologique du lac Tanganika." Ann. Sci. Nat. Zool. ser. 7, T. x. 1890, p. 1.

50. Bouvier, E. L.—"Les Crevettes d'eau douce de la famille des Atyidés que se trouvent dans l'île de Cuba." Bull. Mus. d'Hist. Nat. Paris, T. xv. 1909, p. 329.

51. ,, "Sur la classification des Crevettes de la famille des Atyidés." Bull. Soc. Ent. France, Paris, 1913, p. 177.

52. ,, "Sur les Caractères, les Affinités et les Origines de la Faune atyienne du lac Tanganyika." IX^e Congrès Internat. Zool. Monaco, 1913, p. 572.

53. Braem, F.—"Beiträge zur Kenntnis der Fauna Turkestans.—VII. Bryozoen und deren Parasiten." Trav. Soc. Imp. St. Pétersbourg, vol. xlii. Fasc. 2, Sect. Zool. et Physiol. 1911, p. 3.

54. Brehm, V.—"Die Cladoceren." Wiss. Ergebnisse d. Deutsch. Zentral-Afrika-Exp. 1907–1908, Bd. iii. 1912, p. 167.

55. Bright, R. G. T.—"Survey and Exploration in the Ruwenzori and Lake Region, Central Africa." Geogr. Journ. vol. xxxiv. 1909, p. 128.

56. Browne, E. T.—"On the Freshwater Medusa *Limnocnida tanganicæ* and its Occurrence in the River Niger." Ann. & Mag. Nat. Hist. 7th ser. vol. xvii. 1906, p. 304.

57. ,, "On the Freshwater Medusa *Limnocnida tanganicæ* discovered in the River Niger by the late J. S. Budgett." The Work of J. S. Budgett. Cambridge, 1907, p. 471.

58. Brusina, S.—"Fossile Binnen-Mollusken aus Dalmatien, Kroatien und Slavonien." Agram, 1874. German translation from Rad. Jugoslav. Akad. Agram, vol. xxviii.

59. ,, "Matériaux pour la faune malacologique néogène de la Dalmatie, de la Croatie et de la Slavonie." Djela Jugoslav. Akad. vol. xviii. Agram, 1897.

60. Calman, W. T.—"On two Species of Macrurous Crustaceans from Lake Tanganyika." Proc. Zool. Soc. 1899, p. 704.

61. ,, "Zoological Results of the Third Tanganyika Expedition, 1904–1905.—Report on the Macrurous Crustacea." Proc. Zool. Soc. 1906, vol. i. p. 187.

62. ,, "The Researches of Bouvier and Bordage on Mutations in Crustacea of the Family Atyidæ." Quart. Journ. Micr. Sci. vol. lv. 1910, p. 785.

63. Carson, A.—"The Rise and Fall of Lake Tanganyika." Quart. Journ. Geol. Soc. vol. xlviii. 1892, p. 401.

64. Collin, A.—"Rotatorien, Gastrotrichen und Entozoen Ost-Afrikas." Deutsch-Ost-Afrika, Bd. iv. Berlin, 1898.

65. Crosse, H.—"Faune malacologique du Lac Tanganyika." Journ. de Conch. vol. xxix. 1881, p. 105.

66. ,, "Supplément à la Faune malacologique du Lac Tanganyika." Journ. de Conch. vol. xxix. 1881, p. 277.

67. Cunnington, W. A.—"On a new Brachyurous Crustacean from Lake Tanganyika." Proc. Zool. Soc. 1899, p. 697.

68. ,, "The Third Tanganyika Expedition." Nature, vol. lxxiii. 1905–06, p. 310.

69. ,, "Tanganyika or Tanganika." Geogr. Journ. vol. xxvii. 1906, p. 411.

70. ,, "Zoological Results of the Third Tanganyika Expedition, 1904–1905.—Report on the Brachyurous Crustacea." Proc. Zool. Soc. 1907, p. 258.

71. ,, "On the Nature and Origin of Fresh-water Organisms." Bathymetrical Survey Scottish Fresh-water Lochs, vol. i. 1910, p. 354.

72. ,, "Zoological Results of the Third Tanganyika Expedition, 1904–1905.—Report on the Branchiura." Proc. Zool. Soc. 1913, p. 262.

73. ,, "Zoological Results of the Third Tanganyika Expedition, 1904–1905.—Report on the Parasitic Eucopepoda." Proc. Zool. Soc. 1914, p. 819.

74. ,, "On the Entomostraca of the Albert Nyanza." Ann. & Mag. Nat. Hist. 8th ser. vol. xvi. 1915, p. 80.

75. Daday, E. von.—"Plancton-Tiere aus dem Victoria Nyanza." Zool. Jahrb. Syst. Bd. xxv. 1907, p. 245.

76. ,, "Untersuchungen über die Süsswasser-Mikrofauna Deutsch-Ost-Afrikas." Zoologica, Bd. xxiii. 1910, p. 1.

77. Delachaux, T.—"Cladocères de la région du lac Victoria Nyanza." Rev. Suisse de Zool. vol. xxv. 1917, p. 77.

78. Digby, L. —"On the Structure and Affinities of the Tanganyika Gastropods *Chytra* and *Limnotrochus*." Journ. Linn. Soc. (Zool.) vol. xxviii. 1900–1903, p. 434.

79. Dohrn, H. —"List of the Land and Freshwater Shells of the Zambesi and Lake Nyassa, Eastern Tropical Africa, collected by John Kirk." Proc. Zool. Soc. 1865, p. 231.

80. Douwe, C. van. —"Copepoden des ostafrikanischen Seengebietes." Wiss. Ergebnisse d. Deutsch. Zentral-Afrika-Exp. 1907–1908, Bd. iii. 1912, p. 487.

81. " "Zur Kenntnis ostafrikanischer Copepoden: *Canthocamptus schröderi* (♀), n. spec." Zool. Anz. Bd. xlv. 1915, p. 263.

82. Evans, R. —"A Description of two new Species of *Spongilla* from Tanganyika." Quart. Journ. Micr. Sci. vol. xli. 1898–99, p. 471.

83. Fülleborn, F. —"Ueber Untersuchungen im Nyassa-See und in den Seen im nördlichen Nyassa-Land." Verhandl. d. Gesellschaft f. Erdkunde, Berlin, Bd. xxvii. 1900, p. 332.

84. Germain, L. —"Liste des mollusques recueillis par M. E. Foa dans le lac Tanganika et ses environs." Bull. Mus. d'Hist. Nat. Paris, T. xi. 1905, p. 254.

85. " "Mollusques du lac Tanganyika et de ses environs." Résultats scientifiques des Voyages en Afrique d'Édouard Foà, 1908, p. 612.

86. " "Sur quelques Mollusques recueillis par M. le Dr. Gromier dans le lac Albert Édouard et ses environs." Bull. Mus. d'Hist. Nat. Paris, T. xviii. 1912, p. 77.

87. " "Origine de la Faune fluviatile de l'Est Africain." IX^e Congrès Internat. Zool. Monaco, 1913, p. 559.

88. Giraud, V. —"Description du nouveau genre *Bourguignatia* du Tanganika." Bull. Soc. Mal. France, T. ii. 1885, p. 193.

89. Gravier, C. —"Sur la méduse du Victoria Nyanza et la faune des grands lacs africains." Bull. Mus. d'Hist. Nat. Paris, T. ix. 1903, p. 347.

90. " "La Méduse du Tanganyika et du Victoria Nyanza; sa dispersion en Afrique." Bull. Mus. d'Hist. Nat. Paris, T. xiii. 1907, p. 218.

91. Grogan, E. S., and Sharp, A. H.—"From the Cape to Cairo." New Edit. London, 1902.

92. Guerne, J. de. —"La Méduse du lac Tanganyika." La Nature, T. xxi. 1893, 2^e semestre, p. 51.

93. Günther, A. —"Descriptions of the Reptiles and Fishes collected by Mr. E. Coode-Hore on Lake Tanganyika." Proc. Zool. Soc. 1893, p. 628.

94. Günther, R. T. —"Preliminary account of the Freshwater Medusa of Lake Tanganyika." Ann. & Mag. Nat. Hist. 6th ser. vol. xi. 1893, p. 269.

95. " "A further Contribution to the Anatomy of *Limnocnida tanganyicæ*." Quart. Journ. Micr. Sci. vol. xxxvi. 1894, p. 271.

96. " "Zoological Results of the Third Tanganyika Expedition, 1904–1905.—Report on *Limnocnida tanganicæ*; with a Note on the Sub-species from the Victoria Nyanza." Proc. Zool. Soc. 1907, p. 643.

97. Gurney, R. —"The Origin and Conditions of Existence of the Fauna of Fresh Water." Trans. Norfolk and Norwich Naturalists' Soc. vol. ix. 1913, p. 463.

93. Halbert, J. N. —"Zoological Results of the Third Tanganyika Expedition, 1904–1905.—Report on the Hydrachnida." Proc. Zool. Soc. 1906, p. 535.

99. Harmer, S. F. —"The Polyzoa of the Siboga Expedition." Part i. Livr. lxxv. Leyden, 1915.

100. Hilgendorf, F. —"Die Land- und Süsswasser-Dekapoden Ostafrikas." Deutsch-Ost-Afrika, Bd. iv. Berlin, 1898.

101. Hore, E. C. —"Tanganyika: Eleven Years in Central Africa." London, 1892.

102. Hudleston, W. H. —"On the Origin of the Marine (Halolimnic) Fauna of Lake Tanganyika." Geol. Mag. n. s., dec. 5, vol. i. 1904, p. 337.

103. Hundeshagen, F. —"Analyse einiger ostafrikanischer Wässer." Zeitsch. f. offentliche Chemie. Plauen, 1909, p. 201.

104. Keilhack, L. —"Njassa-Fische gesammelt von Professor Dr. Fülleborn." Mitt. Zool. Mus. Berlin, Bd. v. 1910, p. 91.

105. Kirkpatrick, R. —"Zoological Results of the Third Tanganyika Expedition, 1904–1905.—Report on the Porifera, with Notes on Species from the Nile and Zambesi." Proc. Zool. Soc. 1906, vol. i. p. 218.

106. Koenike, F. —"Die Hydrachniden Ost-Afrikas." Deutsch-Ost-Afrika, Bd. iv. Berlin, 1898.

107. Laidlaw, F. F. —"Zoological Results of the Third Tanganyika Expedition, 1904–1905.—Report on the Turbellaria." Proc. Zool. Soc. 1906, p. 777.

108. Lea, I. —"Descriptions of six new Species of Unionidæ from Lake Nyassa, Central Africa, etc." Proc. Acad. Nat. Sci. Philadelphia, 1864, p. 108.

109. Lenz, H. —"Dekapode Crustaceen Aequatorialafrikas." Wiss. Ergebnisse d. Deutsch. Zentral-Afrika-Exp. 1907–1908, Bd. iii. 1912, p. 121.

110. Man, J. G. de. —"On *Caridina nilotica* (Roux) and its Varieties." Rec. Ind. Mus. vol. ii. 1908–1909, p. 255.

111. Marquardsen, H. —"Die Seen Tanganjika, Moero, Bangweolo." Mitt. a. d. Deutsch. Schutzgebieten, Bd. xxix. 1916, p. 97.

112. Martel, H., et Dautzenberg, P.—"Observations sur quelques mollusques du lac Tanganyika recueillis par le R. P. Guillemé et descriptions de formes nouvelles." Journ. de Conch. 4e ser. T. i. 1899, p. 163.

113. Martens, E. von. —"Recente Conchylien aus dem Victoria Nianza." Sitzb. naturf. Fr. Berlin, 1879, p. 103.

114. ,, "Ueber eine von Dr. Böhm im Tanganjika-See gefundene Qualle." Sitzb. naturf. Fr. Berlin, 1883, p. 97.

115. ,, "Einige neue Arten von Land- und Süsswasser-Mollusken aus Uganda und dem Victoria-Nyansa." Sitzb. naturf. Fr. Berlin, 1892, p. 15.

116. ,, "Beschalte Weichthiere Ost-Afrikas." Deutsch-Ost-Afrika, Bd. iv. Berlin, 1898.

117. Meissner, M. —"Die Moosthiere Ost-Afrikas." Deutsch-Ost-Afrika, Bd. iv. Berlin, 1898.

118. Michaelsen, W. —"Beschreibung der von Herrn Dr. Fr. Stuhlmann am Victoria Nyanza gesammelten Terricolen." Jahrb. d. Hamburg Wiss. Anst. Jahrg. 9, Zweite Hälfte, 1891, p. 29.

119. ,, "Die Regenwürmer Ost-Afrikas." Deutsch-Ost-Afrika, Bd. iv. Berlin, 1898.

120. ,, "Die Oligochaeten Deutsch-Ostafrikas." Zeit. Wiss. Zool. Bd. lxxxii. 1905, p. 288.

121. Michaelsen, W. —"Die Oligochäten des inneren Ostafrikas und ihre geographischen Beziehungen." Wiss. Ergebnisse d. Deutsch. Zentral-Afrika-Exp. 1907–1908, Bd. iii. 1912, p. 1.

122. Moore, J. E. S. —"On the general Zoological Results of the Tanganyika Expedition." Proc. Zool. Soc. 1897, p. 436.

123. " "The Physiographical Features of the Nyasa and Tanganyika Districts of Central Africa." Geogr. Journ. vol. x. 1897, p. 289.

124. " "The Fauna of the Great African Lakes." Science Progress, vol. vi. 1897, p. 627.

125. " "The Fresh-water Fauna of Lake Tanganyika." Nature, vol. lvi. 1897, p. 198.

126. " "On the Zoological Evidence for the connection of Lake Tanganyika with the Sea." Proc. Roy. Soc. vol. lxii. 1897–98, p. 451.

127. " "The Marine Fauna in Lake Tanganyika, and the advisability of Further Exploration in the great African Lakes." Nature, vol. lviii. 1898, p. 404.

128. " "Descriptions of the Genera *Bathanalia* and *Bythoceras* from Lake Tanganyika." Proc. Malac. Soc. vol. iii. 1898–99, p. 92.

129. " "The Molluscs of the Great African Lakes.—I. Distribution." Quart. Journ. Micr. Sci. vol. xli. 1898–99, p. 159.

130. " "The Molluscs of the Great African Lakes.—II. The Anatomy of the Typhobias, with a description of the new Genus (*Batanalia*)." Quart. Journ. Micr. Sci. vol. xli. 1898–99, p. 181.

131. " "On the Hypothesis that Lake Tanganyika represents an old Jurassic sea." Quart. Journ. Micr. Sci. vol. xli. 1898–99, p. 303.

132. " "The Molluscs of the Great African Lakes.—III. *Tanganyikia rufofilosa* and the Genus *Spekia*." Quart. Journ. Micr. Sci. vol. xlii. 1899, p. 155.

133. " "The Molluscs of the Great African Lakes.—IV. *Nassopsis* and *Bythoceras*." Quart. Journ. Micr. Sci. vol. xlii. 1899, p. 187.

134. " "Tanganyika and the Counties north of it." Geogr. Journ. vol. xvii. 1901, p. 1.

135. " "Further Researches concerning the Molluscs of the Great African Lakes." Proc. Zool. Soc. 1901, vol. ii. p. 461.

136. " "To the Mountains of the Moon." London, 1901.

137. " "The Tanganyika Problem." London, 1903.

138. " "Halolimnic Faunas and the Tanganyika Problem." Report British Association, 1906, p. 601.

139. Mrázek, A. —"Die Copepoden Ost-Afrikas." Deutsch-Ost-Afrika, Bd. iv. Berlin, 1898.

140. Nicolas, H. —"Origine marine de certaines espèces de mollusques, en cours de transformation, du lac Tanganyika." Comptes Rendus Assoc. Française Avancement Sci. 1898, 2ᵉ partie, p. 508.

141. Nieden, F. —"Amphibia." Wiss. Ergebnisse d. Deutsch. Zentral-Afrika-Exp. 1907–1908, Bd. iv. 1913, p. 165.

142. Pappenheim, P., und Boulenger, G. A.—"Fische." Wiss. Ergebnisse d. Deutsch. Zentral-Afrika-Exp. 1907–1908, Bd. v. 1914, p. 225.

143. Pelseneer, P. —"Notice sur les Mollusques recueillis par M. le Capitaine Storms dans la région du Tanganyka." Bull. Mus. d'Hist. Nat. Belg. T. iv. 1886, p. 103.

144. Pelseneer, P. —"Halolimnic Faunas and the Tanganyika Problem." Report British Association, 1906, p. 602.

145. Regan, C. T. —"The Classification of the Fishes of the Family Cichlidae.—I. The Tanganyika Genera." Ann. & Mag. Nat. Hist. 9th ser. vol. v. 1920, p. 33.

146. " "A new Cichlid Fish of the Genus *Limnochromis* from Lake Tanganyika." Ann. & Mag. Nat. Hist. 9th ser. vol. v. 1920, p. 152.

147. Rendle, A. B. —"General Report upon the Botanical Results of the Third Tanganyika Expedition, conducted by Dr. W. A. Cunnington, 1904 and 1905." Journ. Linn. Soc. (Bot.) vol. xxxviii. 1907, p. 18.

148. Rhoades, E. L. —"Survey of Lake Nyasa." Geogr. Journ. vol. xx. 1902, p. 68.

149. Rousselet, C. F. —"Zoological Results of the Third Tanganyika Expedition, 1904–1905.—Report on the Polyzoa." Proc. Zool. Soc. 1907, p. 250.

150. " "Zoological Results of the Third Tanganyika Expedition, 1904–1905.—Report on the Rotifera." Proc. Zool. Soc. 1910, p. 792.

151. Sars, G. O. —"Zoological Results of the Third Tanganyika Expedition, 1904–1905.—Report on the Copepoda." Proc. Zool. Soc. 1909, p. 31.

152. " "Zoological Results of the Third Tanganyika Expedition, 1904–1905.—Report on the Ostracoda." Proc. Zool. Soc. 1910, p. 732.

153. " "Zoological Results of the Third Tanganyika Expedition, 1904–1905.—Report on some Larval and Young Stages of Prawns from Lake Tanganyika." Proc. Zool. Soc. 1912, p. 426.

154. Schaudinn, F. —"Rhizopoda Ost-Afrikas." Deutsch-Ost-Afrika, Bd. iv. Berlin, 1898.

155. Schokalsky, J. de, et Schmidt, P. J.—"Aperçu sur les Explorations Scientifiques des Mers et des Eaux douces de l'Empire Russe." Exposition Maritime Internationale de Bordeaux, 1907.

156. Schubotz, H. —"Vorwort." Wiss. Ergebnisse d. Deutsch. Zentral-Afrika-Exp. 1907–1908, Bd. iii. 1912, p. vii.

157. Sieger, R. —"The Rise and Fall of Lake Tanganyika." Quart. Journ. Geol. Soc. vol. xlix. 1893, p. 579.

158. Smith, E. A. —"On the Shells of Lake Nyassa, and on a few Marine Species from Mozambique." Proc. Zool. Soc. 1877, p. 712.

159. " "Diagnoses of new Shells from Lake Tanganyika and East Africa." Ann. & Mag. Nat. Hist. 5th ser. vol. vi. 1880, p. 425.

160. " "On the Shells of Lake Tanganyika and of the Neighbourhood of Ujiji, Central Africa." Proc. Zool. Soc. 1880, p. 344.

161. " "On a Collection of Shells from Lakes Tanganyika and Nyassa and other localities in East Africa." Proc. Zool. Soc. 1881, p. 276.

162. " "Descriptions of two new Species of Shells from Lake Tanganyika." Proc. Zool. Soc. 1881, p. 558.

163. " "Tanganyika Shells." Nature, vol. xxv. 1881–82, p. 218.

164. " "On the Shells of the Albert Nyanza, Central Africa, obtained by Dr. Emin Pasha." Proc. Zool. Soc. 1888, p. 52.

165. " "Diagnoses of new Shells from Lake Tanganyika." Ann. & Mag. Nat. Hist. 6th ser. vol. iv. 1889, p. 173.

166. Smith, E. A. —"On a new Genus and some new Species of Shells from Lake Tanganyika." Ann. & Mag. Nat. Hist. 6th ser. vol. vi. 1890, p. 93.

167. „ "On the Shells of the Victoria Nyanza or Lake Oukéréwé." Ann. & Mag. Nat. Hist. 6th ser. vol. x. 1892, p. 121.

168. „ "Additions to the Shell-Fauna of the Victoria Nyanza or Lake Oukéréwé." Ann. & Mag. Nat. Hist. 6th ser. vol. x. 1892, p. 380.

169. „ "On a Collection of Land and Freshwater Shells transmitted by Mr. H. H. Johnston, C.B., from British Central Africa." Proc. Zool. Soc. 1893, p. 632.

170. „ "Some remarks on the Mollusca of Lake Tanganyika." Proc. Malac. Soc. vol. vi. 1904, p. 77.

171. „ "Zoological Results of the Third Tanganyika Expedition, 1904–1905.—Report on the Mollusca." Proc. Zool. Soc. 1906, vol. i. p. 180.

172. Soar, C. D. —"A Contribution to the List of Hydrachnidæ found in the East African Lakes." Journ. Quekett Club, ser. 2, vol. xi. 1910, p. 109.

173. Sollas, W. J. —"The Origin of Fresh-water Fauna." The Age of the Earth, and other Geological Studies, London, 1905, no. 7, p. 166.

174. Stappers, L. —"Sondages dans le lac Tanganika." Revue Congolaise, Bruxelles, 1913, p. 116.

175. „ "Recherches Bathymétriques sur les lacs Moéro et Tanganika." Ann. Biol. lacustre, T. vii. 1914, p. 83.

176. „ "Composition chimique de l'eau de surface des lacs Moëro et Tanganika." Renseignements de l'Office Colonial, Bruxelles, 1914, p. 189.

177. Stebbing, T. R. R. —"Zoological Results of the Third Tanganyika Expedition, 1904–1905.—Report on the Isopoda Terrestria." Proc. Zool. Soc. 1908, p. 554.

178. Steindachner, F. —"Ueber einige neue Fischarten aus dem Tanganyikasee." Anz. Akad. Wiss. Wien, 1909, p. 399.

179. „ "Beiträge zur Kenntnis der Fischfauna des Tanganyikasees und des Kongogebietes." Sitzb. Akad. Wiss. Wien, Bd. cxx. Abth. i. 1911, p. 1171.

180. Sternfeld, R. —"Reptilia." Wiss. Ergebnisse d. Deutsch. Zentral-Afrika-Exp. 1907–1908, Bd. iv. 1913, p. 197.

181. Stuhlmann, F. —"Vorläufiger Bericht über eine mit Unterstützung der Königlichen Akademie der Wissenschaften unternommene Reise nach Ost-Africa, zur Untersuchung der Süsswasserfauna." Sitzb. Akad. Wiss. Berlin, 1888, p. 1255.

182. „ "Zweiter Bericht über eine mit Unterstützung der Königlichen Akademie der Wissenschaften nach Ost-Africa unternommene Reise." Sitzb. Akad. Wiss. Berlin, 1889, p. 645.

183. „ "Beiträge zur Fauna centralafrikanischer Seen.—I. Südereck des Victoria-Niansa." Zool. Jahrb. Syst. Bd. v. 1891, p. 924.

184. „ "Zur Kenntniss der Fauna central-afrikanischer Seen.—II. Ueber eine neue Art der Arguliden-Gattung *Gyropeltis*." Zool. Jahrb. Syst. Bd. v. 1891, p. 152.

185. „ "Mit Emin Pascha ins Herz von Afrika." Berlin, 1894.

186. Tausch, L. —"Ueber einige Conchylien aus dem Tanganyika-See und deren fossile Verwandte." Sitzb. Akad. Wiss. Wien, Math-Naturw. Classe, Bd. xc. Abth. i. 1884, p. 56.

187. Thiele, J. —"Diagnosen neuer Arguliden-Arten." Zool. Anz. Bd. xxiii. 1900, p. 46.

188. " "Beiträge zur Morphologie der Arguliden." Mitt. Zool. Mus. Berlin, Bd. ii. Heft. 4, 1904.

189. " "Mollusken der Deutschen Zentralafrika-Expedition." Wiss. Ergebnisse d. Deutsch. Zentral-Afrika-Exp. 1907–1908, Bd. iii. 1912, p. 175.

190. Thomson, J. —"To the Central African Lakes and back." Vols. i. & ii. London, 1881.

191. " "On the Geographical Evolution of the Tanganyika Basin." Report British Association, 1882, p. 622.

192. Tornier, G. —"Die Kriechthiere Deutsch-Ost-Afrikas." Deutsch-Ost-Afrika, Bd. iii. Berlin, 1897.

193. " "Neue Liste der Crocodile, Schildkröten und Eidechsen Deutsch Ost-Afrikas." Zool. Jahrb. Syst. Bd. xiii. 1900, p. 579.

194. " "Herpetologisch Neues aus Deutsch-Ost-Afrika." Zool. Jahrb. Syst. Bd. xv. 1902, p. 578.

195. Ulmer, G. —"Süsswasser-Bryozoen von Aequatorial-Afrika." Wiss. Ergebnisse d. Deutsch. Zentral-Afrika-Exp. 1907–1908, Bd. iv. 1913, p. 285.

196. Vávra, V. —"Die Süsswasser-Ostracoden Deutsch-Ost-Afrikas." Deutsch-Ost-Afrika, Bd. iv. Berlin, 1898.

197. Virieux, J. —"Planeton du lac Victoria Nyanza." Voyage de Ch. Alluaud et R. Jeannel en Afrique orientale. Résultats scientifiques. Paris, 1913.

198. Weltner, W. —"Die Cladoceren Ost-Afrikas." Deutsch-Ost-Afrika, Bd. iv. Berlin, 1898.

199. " "Die Coelenteraten und Schwämme des süssen Wassers Ost-Afrikas." Deutsch-Ost-Afrika, Bd. iv. Berlin, 1898.

200. West, G. S. —"Report on the Freshwater Algæ, including Phytoplankton, of the Third Tanganyika Expedition, conducted by Dr. W. A. Cunnington, 1904–1905." Journ. Linn. Soc. (Bot.) vol. xxxviii. 1907, p. 81.

201. " "Phytoplankton from the Albert Nyanza." Journ. Bot. vol. xlvii. 1909, p. 244.

202. White, C. A. —"New Molluscan Forms from the Laramie and Green River groups, with discussion of some associated forms heretofore known." Proc. U.S. Mus. vol. v. 1882, p. 94.

203. " "Tanganyika Shells." Nature, vol. xxv. 1881–82, p. 101.

204. Wissmann, H. von. —"Through Equatorial Africa." (English translation.) London, 1891.

205. Woodward, S. P. —"On some new Freshwater Shells from Central Africa." Proc. Zool. Soc. 1859, p. 348.

33. Descriptions of the Adult, Larval, and Pupal Stages of a New Mosquito from Lord Howe Island, S. Pacific. By Henry F. Carter, Liverpool School of Tropical Medicine *.

[Received September 25, 1920: Read November 16, 1920.]

(Text-figures 1–3.)

The material from which the following descriptions were drawn up was collected by Mr. R. Douglas Laurie, M.A., of the Zoological Department, University College, Aberystwyth, in Lord Howe Island during the summer of 1914. The adult mosquitoes, a male and a female, were reared by him from larvæ and pupæ found in a hole containing water in a fallen tree. The second species, to which mere reference is made, was taken on the wing in a dwelling-house at night.

OCHLEROTATUS LAUREI, sp. n.

A medium-sized, reddish-brown, mosquito with golden-coloured lines on the thorax, and the dorsal surface of the abdomen uniformly dark brown. Proboscis and legs blackish, some or all of the tarsal segments with small pale bands. Male palpi relatively short, scarcely more than half the length of the proboscis.

Head: Integument blackish, the occipital region clothed mainly with narrow, curved, and upright forked scales, but with small areas of creamy-white flat scales laterally; curved scales black and golden, the latter forming a median line, which broadens posteriorly, and a border (composed of a single row of scales) round the eyes; upright scales long and thin, black anteriorly and medially, dark yellowish-brown posteriorly and laterally. Eyes black. Antennæ dark brown, each with the basal segment and base of the second segment yellowish-brown. Proboscis straight, long and slender, black; labellæ small, pointed, testaceous. Palpi black; in the female very short, each with two narrow white rings and a white apex; in the male slender, about half the length of the proboscis, each with a narrow white band at the bases of the four segments, terminal segment about two-thirds the length of the penultimate, no distinct hair-tufts present. Clypeus black, pruinose. *Thorax*: Integument reddish-brown, clothed with dark brown and golden, narrow, curved scales; the golden scales are arranged in a definite manner as follows:—a narrow border round the anterior edge, two small more or less circular shoulder-spots, a median line broad anteriorly and gradually tapering to a point near the middle of the scutum, two

---

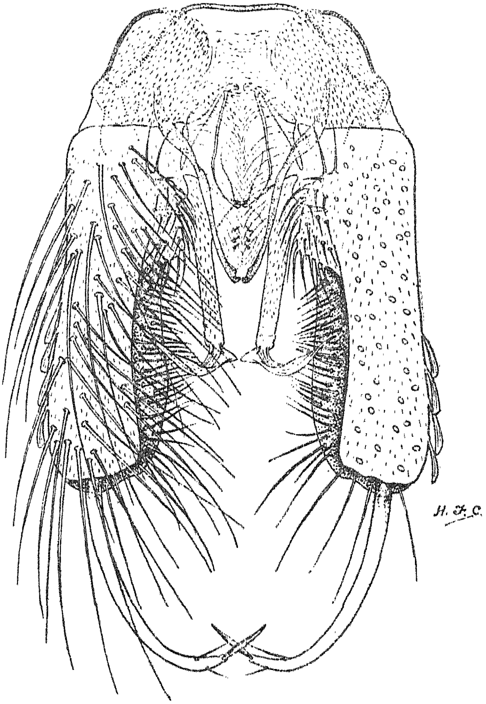
* Communicated by R. D. Laurie, F.Z.S.

narrow dorso-lateral lines extending parallel from the scutellum to a spot slightly beyond the centre of the scutum, then becoming somewhat broader and curving outwards to meet the edge of the scutum about the anterior third, two very short admedian lines immediately before the bare space in front of the scutellum, and lastly, a few scattered scales laterally over the roots of the wings. Prothoracic lobes dark brown, conical, widely separated dorsally, with black bristles anteriorly, and intermingled, curved, golden, and creamy flat scales centrally and posteriorly. Scutellum lighter in colour than the scutum, with sparsely arranged golden, curved scales; border bristles black. Pleuræ dark brown with patches of creamy-white flat scales. *Abdomen*: Integument dark brown. Dorsal surface in the female covered with dark, almost black, flat scales; in the male similar, but with traces of pale lateral basal spots (each formed of a few cream-coloured scales) on the 5th, 6th, and 7th segments; ventral surface in both sexes dark brown, with a pair of large creamy-white lateral basal spots on each segment. Terminal segment of female paler brown, with moderately long cerci. *Wings*: Veins rather densely clothed with dark brown scales, the lateral scales somewhat broadly linear. Fork cells with their bases almost level, the first cell long and narrow, about three times as long as the petiole, the second wider, about twice as long as the petiole; posterior cross-vein about one and one-half times its own length distant from the median cross-vein. *Legs*: Dark brown, blackish. Fore and middle femora each with a narrow line of cream-coloured scales on the ventral surface, basal half of each hind femur broadly cream-coloured, apices of femora with small, yellowish spots. Tibiæ with inconspicuous yellowish knee-spots. First and second tarsal segments of the fore and middle legs with incomplete narrow, basal, whitish bands, tarsal segments of hind legs with basal, white bands. Ungues of female all equal and uniserrate; of fore and middle legs of male unequal and uniserrate, of hind legs of male small, equal, and uniserrate.

Length: Female approximately 5·5 mm., male 5·0 mm.; length of wings of female 5·2 mm., length of wing of male 4·5 mm.

Male Hypopygium (text-fig. 1).—Side-pieces long and narrow—from three to four times as long as the width at the extreme base,—with prominent basal and apical lobes. Dorsal surface of side-piece moderately hairy, the hairs relatively short towards the base, longer apically and laterally; ventral surface with numerous, long, curved hairs; outer margins with a few scales. Basal lobes subquadrate, bearing numerous strong, short hairs; apical lobes large, extending backwards to the basal lobes, with densely arranged, short, inwardly projecting hairs. Terminal clasp-segment slender, comparatively weak, with a long terminal spine and two short delicate hairs slightly before the apex. Tenth sternites (harpes) slender, strongly chitinised, slightly recurved at the tips; connecting membrane with three small spines on each side towards the apex. Claspettes (harpagones) large, rather more than half the length of the side-pieces, each with a conspicuous, attenuated, membranous foot-like appendage. Ædeagus (unci) separate distally, without serrations or teeth.

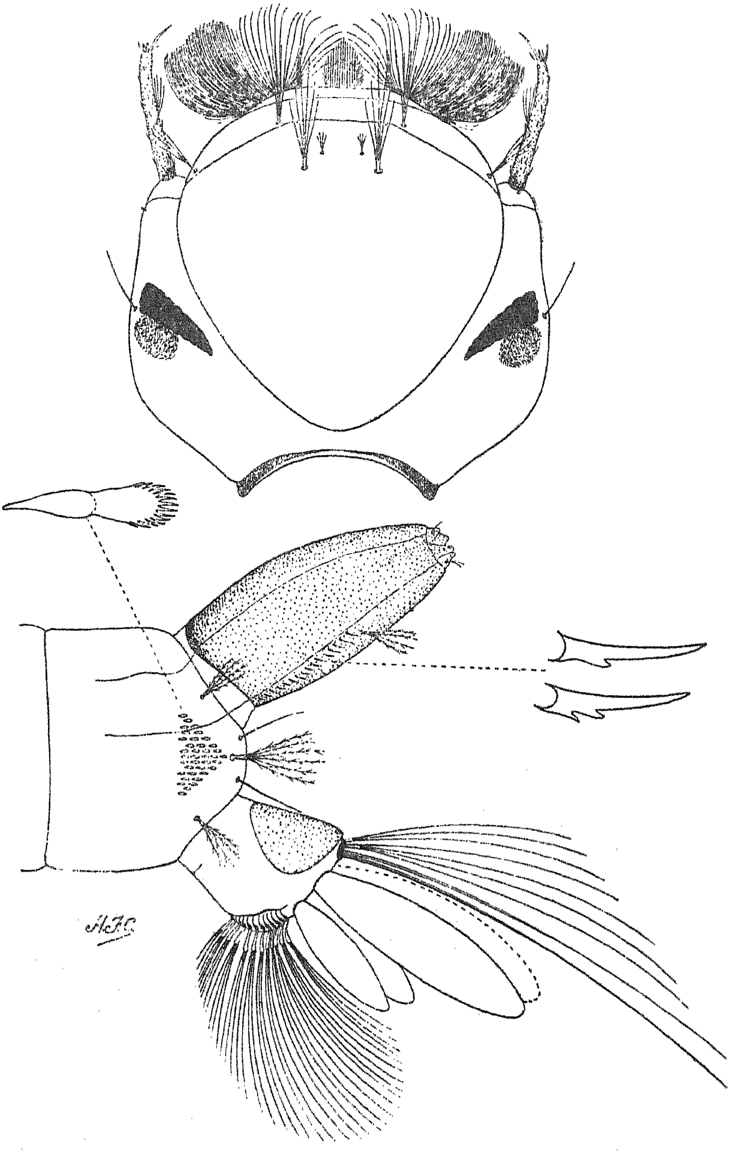
Text-figure 1.



Male hypopygium of *Ochlerotatus laurei*, sp. n. × 120.
(Hairs of portion of right side-piece omitted.)

Larva (text-fig. 2).—Relatively stout, about 7 mm. in length. Head rounded, slightly narrowed before the eyes; antennæ cylindrical, sparsely covered with minute spines and bearing four or five longer spines at the apex; antennal tuft small, centrally situated, composed of four simple hairs arising from a common stem. Dorsal hairs not feathered, compound, the anterior pair each composed of four hairs, the small median of four and the posterior of five or six; ante-antennal tuft formed of four to six hairs. Mental plate triangular in shape, armed with from 12–14 teeth on each side; the terminal tooth longer and broader than the rest, the apical lateral teeth elongate and somewhat crowded

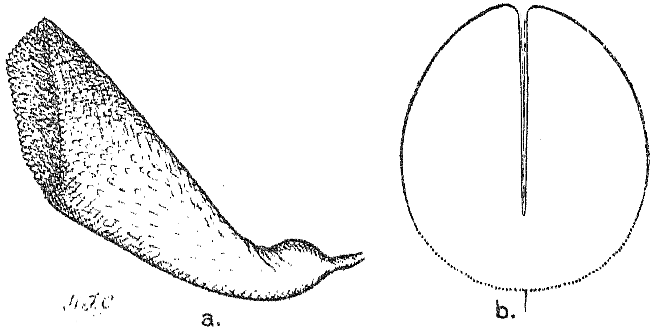
Text-figure 2.



Head and anal extremity of larva of *Ochlerotatus laurei*, sp. n.

together, the posterior lateral teeth broader (almost triangular near the base) and more widely separate, the last tooth small and remote. Thorax wider than long, hairs moderate, feathered, the stouter, multiple ones each consisting of from 8–10 hairs. Abdomen somewhat stout. Eighth abdominal segment as shown in text-fig. 2, the lateral comb composed of about fifty slightly chitinised scales arranged to form a triangular area; each comb-scale is somewhat elongate and is armed apically with a fringe of spinules. Air-tube about twice as long as broad: pecten composed of some 16 evenly spaced teeth—each pointed and with one or two lateral projections,—the most distal tooth situated about half-way along the tube. Hair-tuft of the air-tube arising immediately beyond the last spine of the pecten and composed of four or five feathered hairs. Anal segment as long as its greatest width, the chitinous plate rather small, not completely encircling the segment; upper pair of papillæ large, about twice the length of the anal segment, lower pair smaller, scarcely exceeding the length of the segment. Dorsal hairs four in number, the upper pair compound composed of 3–4 hairs each, the lower pair longer and apparently single; ventral brush well developed, composed of 14 or 15 compound hairs.

Text-figure 3.



a. Air-trumpet (× 80), and **b.** Paddle (× 45) of pupa of *Ochlerotatus laurei*, sp. n.

Pupa: Anterior region (cephalo-thoracic mass) elongate, subpyriform, compressed ventrally and posteriorly; respiratory trumpets (text-fig. 3 *a*) conical, their apices obliquely truncate. Abdomen relatively stout with weak hairs; dorsal, admedian, pair of multiple hairs of the first segment each composed of about ten short, branched, hairs; second segment with a pair of smaller and less complex multiple, admedian, lateral hairs, and also a pair of longer, single or double, dorso-hairs. Remaining segments with similar dorso-lateral hairs, the seventh and eighth segments, in addition, with a short compound hair (that on the eighth segment formed of 10–12 simple hairs) arising from each of the dorso-antero-lateral angles. Paddles (text-fig. 3 *b*) large, ovoid, each with a short terminal hair.

Mr. Laurie supplied the following data regarding this mosquito:—"Mosquito larvæ and pupæ from a hollow in a fallen tree-trunk. Sea-level. The hollow was about 12 ins. × 4 ins. and 4 ins. deep, and contained water. The larvæ and pupæ were removed and kept in captivity (7. 14), and two adults emerged (a male on 18. 7. 14 and a female on 21. 7. 14) before we left the Island."

This species, which I have much pleasure in dedicating to its collector, is a member of the genus *Ochlerotatus* in the most restricted sense; it resembles *O. eatoni* Edw. from the Madeira Is., in regard to the length of the male palpi. In general facies it somewhat resembles *O. japonicus* Theo., and apparently is related to the Asiatic group of species formed by the last-named mosquito, *O. macfarlanei* Edw., *O. pulcriventer* Giles, *O. oreophilus* Edw., etc.

Five examples of a second and probably undescribed species of *Ochlerotatus* were also captured by Mr. Laurie in a dwelling-house on the island. This species is dull brown in colour, and, with the exception of yellowish lateral abdominal spots, is devoid of ornamentation. Unfortunately, the specimens obtained were all females, and therefore until more material is available it is advisable to refrain from attempting an exact diagnosis.

References.

EDWARDS, F. W.—"Eight new Mosquitoes in the British Museum Collection." Bull. Ent. Res. vi. p. 357 (1915–1916).

" " "Notes on Culicidæ, with descriptions of new Species." Bull. Ent. Res. vii. p. 201 (1916–1917).

Liverpool, July 1917.

34. The Life-History and Habits of the Yellow Dung-Fly (*Scatophaga stercoraria*); a possible Blow-Fly Check. By G. S. Cotterell. With a Preface by Prof. Maxwell Lefroy, F.Z.S.*

(Text-figures 1–14.)

[Received October 19, 1920: Read October 19, 1920.]

PREFACE.

This paper is an account of work undertaken to complete an inquiry into Blow-fly control, of which a partial account has already been published by Mr. A. M. Altson in the Proceedings of the Zoological Society, 1920, p. 195. Of the three important controls of Blow-fly in England, Mr. Altson has already dealt with the two common parasites: the present paper deals with what we believe to be the most important direct enemy of the adult fly, a check which appears to be very effective in this country. The Yellow Dung-fly first showed itself in our work at the Zoological Society in 1915 in connection with methods of trapping flies: it came in numbers, persistently eating the adult Blow-flies, and seriously interfered with experiments out of doors. My observations since show that while the fly preys on a large variety of Diptera, it specially attacks *Calliphora* and *Musca*. It is a constant and general feeder on the common species of Blow-fly in England throughout the season.

The author of this paper undertook the investigation, and submitted this paper as a thesis for the Diploma of the Imperial College: he also investigated the best means of transporting this species to countries where Blow-fly is a serious pest to sheep, in the hope that it might be possible to utilise it as a check on Blow-fly. This has not been possible as yet, but the species seems to have much value in this connection, and its habits as a maggot and an adult are so harmless that it is to be hoped it will eventually be made use of.—H. M. Lefroy.

Introduction.

The study of the life-history and habits of the Yellow Dung-fly was first commenced in October 1919, at a time when the Blow-fly problem was receiving a great deal of attention and the discovery of an efficient control was sought for.

In conjunction with other methods of control then under investigation, that of the Yellow Dung-fly, as a predator on the Blow-fly, was also studied.

The adult fly was identified for me by Mr. Edwards, of the Natural History Museum, South Kensington, as *Scatophaga*

---

* Communicated by Prof. Maxwell Lefroy, F.Z.S.

stercoraria L., belonging to the family Cordyluridæ of the Acalyptrate Diptera.

A description of the species is given in a monograph by Becker, which is at present the standard work on the classification of the family Cordyluridæ.

Both sexes vary from very large and robust flies to small varieties. The largest measures 15 mm. in length and the smallest 8 mm. The span of the wings is over double the length.

The head is globular; the eyes oval, brown, and separated in both sexes by an area equal to half the width of the head. The frontal stripe is rich yellowish brown in the male, dull yellow in the female. The frontal margins of the orbits, cheeks, and face are yellow. The facial bristles are strong; antenna black, and the arista bare except for the upper third, which is feathered.

The thorax of the male is marked with longitudinal stripes on the dorsal surface. There is a bunch of light yellow hairs under each wing. The thorax of the female is coloured darker, the stripes more marked, and the hairs below the wings are absent. Both sexes have more than two rows of acrostical bristles, and well-marked scutellar bristles.

The wings are slightly yellow; anterior cross-veins very distinct, with a smoky coloration round them.

The femora are covered with long yellow hair in the male, especially the anterior pair; other parts yellow but not hairy. In the female the femora are dark and clothed with a few dark hairs.

The abdomen of the male is yellow and very hairy. In the female yellow-green and not hairy. The male abdomen is cylindrical, terminating bluntly. There is a dark area on the ventral surface of the fifth segment marking the entrance to the male genital atrium. In the female it is short, broad at the base and conical, becoming more or less oval when gravid.

The female is smaller than the male and darker, owing to the absence of the yellow hairs. The legs of both sexes are bristly and the pulvilli well developed.

The sexes are distinguished by the size, difference in colour, shape of the abdomen, and the black area on the ventral surface of the abdomen of the male.

There are nineteen British species of the genus, but I have never observed any other breeding in dung.

S. merdaria is the nearest related species, but is distinguished by both sexes being dirty green in colour and by there being only two rows of dorso-central bristles on the thorax.

S. scybalaria is distinguished by the colour of the third antennal joint, which is reddish brown.

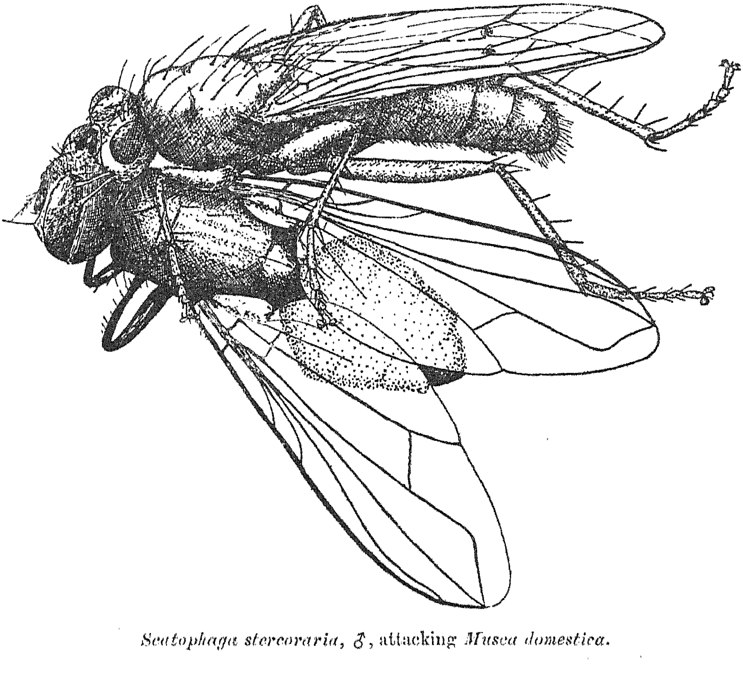
Scatophaga stercoraria is widely distributed. It occurs as far north as Nova Zembla and Siberia, and as far south as North and South Africa and the Canary Islands. It is common throughout Europe and is found in Asia Minor. I have seen no mention of it occurring in India or Australia.

It is evidently both a temperate and sub-tropical species.

Adult Feeding.

Both sexes of the adult fly are predaceous on other Diptera. The prey is never caught on the wing, but usually at the moment of settling. The captured fly is grasped firmly by the middle and hind legs, the bristles of the legs helping to make a firmer grip. The prey is caught in such a fashion as to bring both flies in an upright position and the heads one above the other. In this position the wings of the victim are useless, its legs being the only active part. The proboscis is then pressed against the neck and a puncture made through both sides. Attacked flies may all be seen to have the neck stretched and a distinct hole right through it. In this way the nerve-cord is either cut or damaged, causing a partial paralysis. The contents of the thorax are then sucked out, at the junction of the neck, as far as the proboscis will reach. A large amount of saliva is secreted during these operations, probably acting as a solvent. The head is then turned round by means of the front legs, bringing the oral margin uppermost. Another puncture is made inside the oral margin, and the contents of the head, including the eye-pigment, are also sucked out. Access to the other parts of the thorax is obtained through

Text-figure 1.



Scatophaga stercoraria, ♂, attacking *Musca domestica*.

the thinly-chitinised membranes between the coxæ and thorax. The fly is then turned completely round, bringing the ventral surface of the abdomen uppermost and the head in a posterior position. The contents of the abdomen are then sucked out through punctures between the sternites.

This order of feeding is invariably carried out, but, when food is abundant, the parts are only partially sucked out, the abdomen often not being touched.

Attraction for more food from one victim apparently ceases when struggling has ceased.

Both sexes are very strong in flight and are capable of flying short distances, grasping flies as large as themselves.

Adult Mouth-parts.

On account of its predaceous habits the mouth-parts are modified accordingly.

Externally the proboscis is of the Muscid type, *i. e.* the ordinary labella consisting of the fused inner lobes of the labium, the pseudo-tracheæ, the labrum-epipharynx, hypopharynx, and maxillary palpi. These structures are identical with those found in *Musca domestica* or *Calliphora erythrocephala*, in which the proboscis is adapted for licking. The only modifications due to its predaceous habit are found in the internal chitinised structures of the labellum, or oral disc, and haustellum.

The structure of the rostrum, or proximal portion of the proboscis, is identical with that of *C. erythrocephala* as described by Lowne. The main chitinised structure is the fulcrum (text-fig. 2, *a*) enclosing the pharynx. This has been compared by Kraepelin to a Spanish stirrup-iron with a double foot-plate, the foot-plate being posterior and the toe at the lower end. The whole structure of the rostrum resembles that of a truncated cone with the apex downwards.

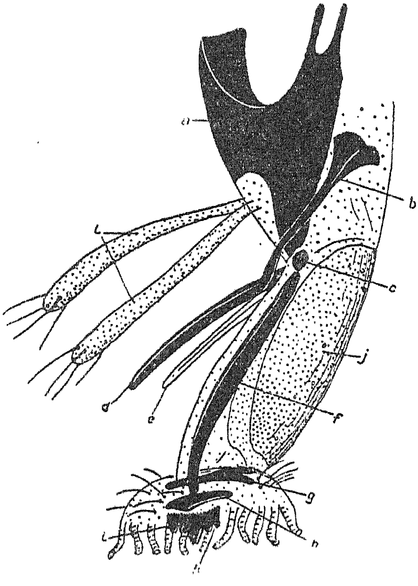
The haustellum or arm of the proboscis is cylindrical in shape. Proximally it is attached to the lower end of the rostrum, and distally to the oral disc. It is enclosed on its lateral and ventral sides by a convex sclerite, the theca (text-fig. 2, *j*). This articulates proximally with the fulcrum and distally with the furca (text-fig. 2, *g*), a tri-radiate sclerite forming the chief internal skeletal structure of the oral disc.

The labrum-epipharynx (text-fig. 2, *d*) and hypopharynx (text-fig. 2, *e*), enclosing the salivary duct, lie over the dorsal portion of the haustellum as in the House-fly.

The oral disc consists of two lobes united posteriorly by a ball-and-socket joint, each grooved on its oral surface by a number of pseudotracheæ (text-fig. 2, *k*). The oral aperture is situated between the lobes at their point of junction. A space below the mouth is kept open by a pair of sclerites, the discal sclerites (text-fig. 2, *h*), deeply embedded in the oral disc. These sclerites are united posteriorly, forming a **U**-shaped structure. This space is the oral pit, and the common trunks of the pseudotracheæ open into this.

Up to this point the structure, except for minor details, is identical with that of the Blow-fly or House-fly. In addition, however, the haustellum is strengthened by a pair of long, chitinised rods (text-fig. 2, *f*), articulating proximally with the fulcrum and distally with the discal sclerites. These occur also in the House-fly and Blow-fly, but are only very slender rods. They play an important part in the articulation of the oral disc. In this case the oral disc is extremely mobile and used for rasping as well as sucking, therefore the rods are more strongly developed. These rods are called paraphyses by Lowne in his description of the Blow-fly.

Text-figure 2.



Mouth-parts of adult:—*a*, fulcrum; *d*, labrum-epipharynx; *e*, hypopharynx; *f*, rods; *g*, furca; *h*, discal sclerite; *i*, teeth; *j*, theca; *k*, pseudotracheæ.

The paraphyses articulate distally with the discal sclerite: thus, there are two articulation points between the haustellum and oral disc—the first between the theca and furca, and the second between the paraphyses and the discal sclerite.

To each arm of the discal sclerite a set of teeth is attached (text-fig. 2, *i*). Each set consists of five teeth, the middle one being the most prominent. They are placed on each side of the oral aperture between the two lobes of the oral disc. They probably correspond to the teeth in the House-fly, forming the lateral edges of the gutters or continuations of the common trunks of the united pseudotracheæ described by Graham-Smith. There are three rows on each side of the oral pit in the House-fly, but only one pair on each in *Scatophaga*. They function to a very small extent for rasping in the House-fly, and in *Scatophaga* they exist essentially for rasping. If this point is correct, the mouth-parts are identical with those of the sucking Muscids, except for certain modifications of the chitinised structures, particularly of the paraphyses and teeth, in accordance with its predaceous habits.

The method of sucking is similar to that of the Blow-fly or House-fly. The liquid food is sucked up through the pseudotracheæ into the oral pit and so into the mouth.

By the alternate upward and downward movement of the paraphyses the oral disc is worked in a backward and forward direction, and, consequently, a rasping is caused by the teeth on any surface they are in contact with. In this manner the thinly-chitinised parts of other Diptera are easily punctured. The internal tissues are broken down by further rasping, and apparently partially dissolved by the large amount of saliva secreted. The liquid food is then sucked up through the pseudotracheæ.

The theca serves not only as an external skeleton to the haustellum, but also protects it from whatever damage it might incur from coming in contact with the jagged edges of chitin when inserted in a hole in its victim.

Breeding Media.

The breeding media consist entirely of excrement providing a sufficient consistency for the larva to complete its life without it becoming dry. This includes human excrement, poultry, sheep and cattle excrement, and horse excrement. The last-mentioned is very rarely used for oviposition. Sheep and cattle excrement is preferred chiefly on account of its viscosity and the amount obtainable in pastures. Cattle excrement was used in the breeding-jars in the laboratory.

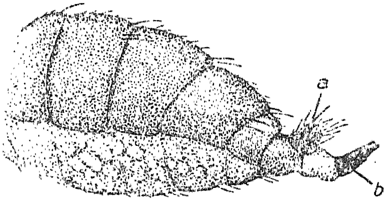
(At the Royal Naval Cordite Factory at Holton Heath a large mass of sludge accumulated from septic sewage tanks: this sludge was in the open, and was about the consistency of fresh cow-dung; it contained an enormous number of this fly in all stages of development, and formed a very suitable breeding medium. I believed that the marked absence of House-flies and Blow-flies at Holton Heath was in part due to this, but I had no direct evidence.—H. M. L.)

Female Genitalia and Method of Oviposition.

As seen externally, the apex of the abdomen of the female ends in two setiferous lobes (text-fig. 3, *a*), between which the anus opens. Below this again is the retractile ovipositor (text-fig. 3, *b*). This consists of a pair of chitinised blades attached, proximally, to a membranous tube. The whole of this can be retracted within the abdomen. The blades are pointed and, when placed together, form a groove. The common oviduct, which is very large, opens into it.

When oviposition is about to take place, the abdomen is stretched out horizontally with the ovipositor extruded. In this position an egg is passed down into the groove formed by the juxtaposition of the two blades of the ovipositor. Ovipositor and egg are then pressed down into the dung obliquely. The blades are pulled apart and the egg released.

Text-figure 3.



Abdomen of female *S. stercoraria*, with genitalia extended.

The eggs are more or less scattered over the surface of the dung, but ten or fifteen or more may be deposited in one small area, particularly where there is a crack or a crevice where the softer parts of the dung are exposed.

Fresh dung is preferred by the females for oviposition, but occasionally eggs are laid in dung a week or more old. In this case the crust on the surface of the dung is too hard for the ovipositor to be inserted deeply, and eggs are often seen only half buried. This does not prevent the egg from hatching, but the larva usually has difficulty in getting through the hardened crust of the dung.

Oviposition occasionally takes place with the male *in situ*, in which case the male removes his abdomen from that of the female, and, instead of clasping her with his two front pairs of legs, drops back clasping her only with the front pair. The female then can manipulate her abdomen freely whilst the male follows her about.

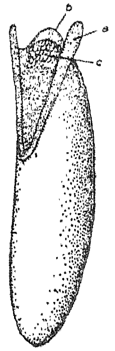
When a female is gravid, the abdomen is so distended as to make her practically incapable of flight. The abdomen is reduced to nearly a fourth its size when oviposition has taken place.

The Egg.

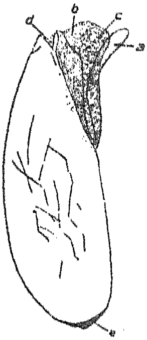
The egg is creamy-white when first laid, becoming darker as the incubation period increases. It measures from 2 to 3 mm. in length and is slightly curved.

It is especially characteristic in having two wing-like extensions of the chorion at its anterior end (text figs. 4 & 5, *a*). These are covered with extremely short setæ on their under surfaces, and serve as a support in the dung. The egg is laid obliquely at an angle of from 15° to 25° with the surface of the dung, so that the two extensions lie flat on the surface. The micropyle (text-figs. 4 & 5, *c*) is situated between the extensions, and is drawn out into a short crest (text-figs. 4 & 5, *b*) at the anterior end between the two extensions. Its surface is finely sculptured. The two extensions and the micropyle are all exposed on the surface. The wall at the base of the egg (text-fig. 5, *e*) is thickened, giving greater strength, as this is the part of the egg which first comes into contact with the dung when oviposition is taking place. The egg is broken by means of a transverse split behind the micropyle (text-fig. 5).

Text-figure 4.



Text-figure 5.



Text-fig. 4.—Egg of *S. stercoraria*, showing supporting wings.
Text-fig. 5.—Hatched egg of *S. stercoraria*.

In summer the whole surface of a deposit of cow-dung may be seen covered with the wing-like extensions of the eggs. The incubation period varies from one to two days according to temperature. This period is much more constant than other periods in the life-history, as temperature is the only governing factor.

The newly-hatched larva breaks the egg behind the micropyle, crawls out on to the surface of the dung, and seeks a convenient crack by which to gain access to the softer parts of the dung. This may take some considerable time if the dung has been deposited for some time, and consequently become dry on the surface.

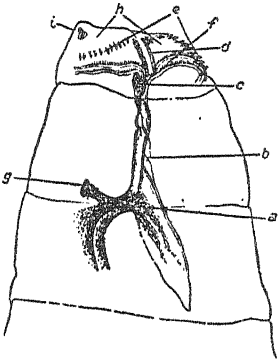
A number of newly hatched larvæ perish through not getting in before they starve.

The Larva.—First Instar.

The larva immediately after hatching measures from 2 to 3 mm. in length. The body is cylindrical, composed of twelve segments, and generally tapers to a point at the anterior end. The posterior end is truncate, forming the anal plate. In this stage the larva is metapneustic, the two spiracles being placed side by side on the anal plate. Each consists of a chitinised ring, situated on a pair of short projections from the anal plate, enclosing two slit-like apertures. The anal plate is bordered by a number of tubercles, the position of which will be described in a later instar.

The first four segments are devoid of spines. Very delicate spines occur on the anterior border of each segment from the fifth posteriorly. The area covered on each segment increases proceeding posteriorly, the whole surface of the last two segments being uniformly covered.

Text-figure 6.



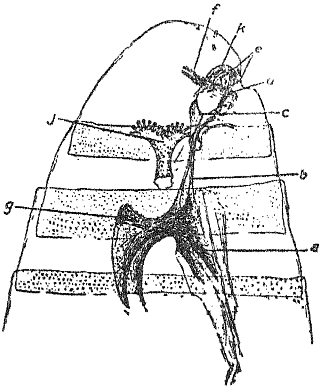
Larva of *S. stercoraria*. 1st instar.

The first segment is divided dorso-ventrally by a cleft forming the two oral lobes (text-fig. 6, *h*). Each lobe carries a pair of sense tubercles (text-fig. 6, *i*). In addition, the ventral surface of the first segment is provided with a transverse row of strong backwardly-curved spines (text-fig. 6, *e*). These are locomotory in function. Keilin mentions them as being present in the first instar larva of *Musca assimilis*. Below the spines there are two channels running more or less parallel with each other. They originate at the mouth, and run out laterally over the ventral surface of the first segment. They are fringed with hair, and direct the liquid food towards the mouth (text-fig. 6, *f*).

The chitinised mouth-parts are slender. Commencing posteriorly there are a pair of **U**-shaped sclerites (text-fig. 6, *a*) with the arms directed backwards. The anterior end of each is extended (text-fig. 6, *b*) for articulation with a large median sclerite (text-fig. 6, *c*). The posterior sclerites, which correspond to the lateral pharyngeal sclerites of the full-grown larva, are united dorso-laterally by a chitinised band (text-fig. 6, *g*). A pair of sclerites are also found embedded in the first segment (text-fig. 6, *d*). These probably correspond to the buccal sclerites or hooks of the full-grown larva. They articulate at their bases with the median sclerite and give rigidity to the oral lobes.

The hooks of the second instar appear behind those of the first a few hours before ecdysis, and become functional as locomotory organs (text-fig. 7).

Text-figure 7.



Larva of *S. stercoraria*. 1st and 2nd instars.

The anterior and posterior spiracles and the remainder of the mouth-parts of the second instar do not appear until just before the moult. An entirely new set of mouth-parts can be seen in a preparation made an hour or so before the moult.

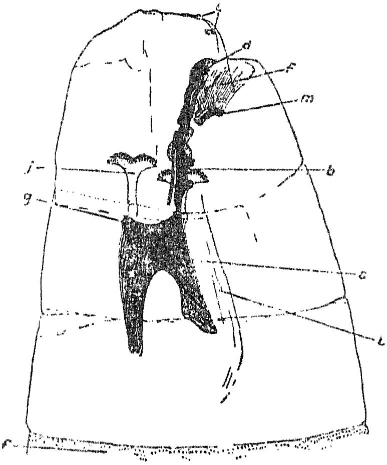
Ecdysis takes place on the first or second day after hatching, the instar lasting from one to two days.

During this instar the larva is very active. In the jars used in the laboratory, occasionally the larvæ hatched out into too liquid dung to allow of a sufficient supply of air below the surface. They were observed to be hanging on to the surface-film with their posterior spiracles exposed, disappearing on being disturbed, reappearing later in the same place. On one occasion the dung remained sufficiently moist to necessitate this during the first two instars. It was only when the third instar was reached that a sufficient air-supply was obtainable below the surface. Probably under natural conditions, where the dung is exposed to wind and other drying factors, it would dry up to a sufficient consistency for the larva to commence living a normal existence buried in the dung itself.

The Larva.—Second Instar.

After the first ecdysis the larva increased considerably in size. It measures from four to six millimetres in length. The general shape of the body and the number of segments remain constant throughout larval life. It is now amphipneustic, being provided with an anterior pair of spiracles (text-fig. 8, *j*) in addition to the posterior pair. The anterior spiracles are situated at the junction of the second and third segments, and will be described in detail in the following instar. The posterior pair are identical with those described in the preceding instar.

Text-figure 8.



Larva of *S. stercoraria*. 2nd instar.

The locomotory spines on the first segment in the previous instar have now disappeared. Spines similar to those of the first instar but proportionately larger occur on each segment behind the fourth. They are concentrated on the anterior border of the fifth, sixth, and seventh segments, but the area covered increases posteriorly. The last few segments are uniformly covered.

The first segment is similar to that described previously, but the locomotory spines are absent. Also the two parallel channels converging into the mouth are now replaced by a number of channels radiating from the mouth over the ventral surface of the oral lobes (text-fig. 8, *f*).

The chitinised mouth-parts have no similarity with those described previously, except for the structure of the lateral pharyngeal plates (text-fig. 8, *a*). These are similar in structure, but are more strongly chitinised and longer in proportion to their breadth. They are united dorsally by a chitinised band, and ventrally by a thinly-chitinised membrane forming the floor of the pharynx (text-fig. 8, *l*). The median piece is replaced by a pair of chitinised rods, the intermediary sclerites (text-fig. 8, *b*), which are united transversely by a bar of chitin. Dorsal to each intermediary sclerite and lying close up to each there is a slender chitinised rod.

The buccal sclerites are elongate and spoon-shaped (text-fig. 8, *d* & text-fig. 9). The exterior lateral edge of each bears four teeth. Ventrally, and at the base of the hooks, there are a pair of short chitinised rods (text-fig. 8, *m*) which support the oral opening.

The buccal sclerites of the third instar appear dorsally to those of the second instar two days before ecdysis, becoming fully chitinised and functional one day before ecdysis. The remainder of the mouth-parts do not become fully chitinised until a few hours before ecdysis. A complete second set of mouth-parts was never definitely observed at this moult, but as all the mouth-parts of the first instar are thrown off, the same may be taken for granted to occur here. The new anterior and posterior spiracles can also be seen underlying those of the present instar.

The second ecdysis takes place on the third and fourth day of larval life, this period lasting from 36 hours to 3 days.

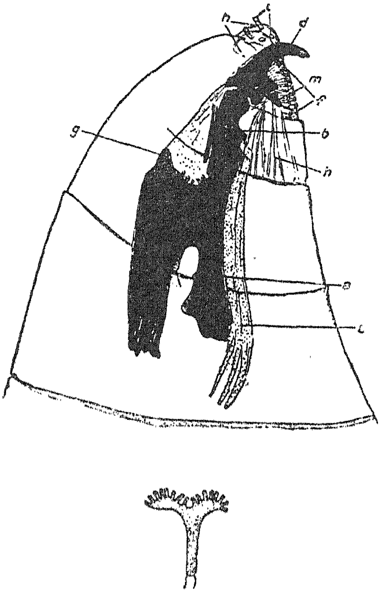
The Larva.—Third Instar.

In the third and final larval instar the larva increases greatly in size, measuring, when full-grown and fully-extended, from one to one and a half centimetres in length. The general external shape is similar to that described in the preceding instars.

The anal plate (text-fig. 11) is surrounded by twelve tubercles. The two largest are situated further forward than the rest on the ventral surface of the last segment immediately behind the anus. The remainder are situated on the border of the anal plate, eight laterally (four on each side) and two dorsally. In addition, there are three situated on the anal plate itself below the spiracles.

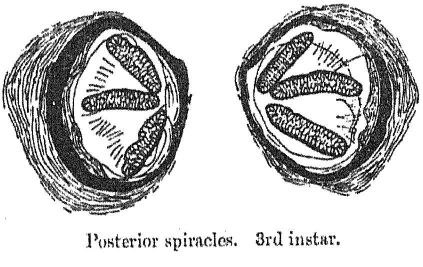
Spines (text-fig. 12) occur on each segment from the fifth segment posteriorly, concentrated on the anterior border. The last few segments are uniformly covered. A belt of spines also occurs round the middle of the fourth segment. The anterior borders of the four anterior segments bear a number of small projecting plates (text-fig. 13) arranged in a number of concentric rings round the segment. Each plate lies against the side of the body, but is hinged anteriorly and can be pushed away from the body. These help to give the first segments a grip when pushed into the dung, but they can also be pulled in against the side of the body if the larva wishes to withdraw its anterior segments. They are to be contrasted with the spines covering the remainder of the body, which also help to give the segments a grip on the sides of the larval burrow, but, being fixed, prevent a backward movement. If the anterior segments were covered with these, the larva, once having pushed its head in one direction, would be obliged to continue whether it wanted to or not. The hinged plates give it a chance to make a second investigation in another direction provided that it has not gone too far.

Text-figure 9.



Larva of *S. stercoraria*. 3rd instar.

Text-figure 10.



Posterior spiracles. 3rd instar.

The first segment is divided into two oral lobes with radiating food-channels on their ventral surfaces as in the preceding instar.

The chitinised mouth-parts are similar in general structure to those of the second instar, but are proportionately stronger. The lateral pharyngeal sclerites are longer and more deeply cleft (text-fig. 9, *a*). The intermediary sclerites are much thickened and shortened. The buccal sclerites (text-fig. 9, *d*) have no similarity with those of the second instar. They have lost the spoon-shaped structure, and are now a pair of stout ventrally curved hooks. They are pointed anteriorly and thickened where they articulate with the intermediary sclerites. They project externally over the oral opening.

The anterior spiracles (text-fig. 9) are situated laterally at the junction of the second and third segments. They consist of a short chitinised trunk, projecting forwards and externally from the junction of the segments. The trunk divides into two lobes, each lobe bearing usually eight papillæ, making sixteen in all. Each papilla is pierced by a small lumen for the ingress of air. The number of papillæ varies from sixteen to eighteen in different larvæ.

The posterior spiracles (text-fig. 10) are situated side by side in the middle of the anal plate. Each consists of a chitinised ring, situated on a short projection, enclosing three slit-like apertures. The apertures are bordered by inwardly projecting filaments serving as a sieve for the incoming air. These spiracles are the most necessary to the larva, being those it keeps above the surface-film when living in very liquid dung. The respective anterior and posterior spiracles are connected by two lateral longitudinal tracheal trunks. The lateral trunks are connected, soon after their origins from the posterior spiracles, by a transverse trunk. In addition the longitudinal trunks give off small branches in each segment.

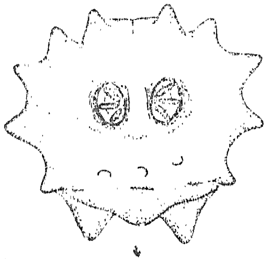
The anus is situated on the triangular plate on the ventral surface of the last segment. This plate is devoid of spines, and appears to be glandular in structure.

The third instar period takes from 6 to 9 days, pupation taking place on the ninth to twelth day of larval life.

The larva is active only during the first two days of this instar, after which it seeks the drier parts of the dung or the soil, preferably the latter. During the inactive period it changes from a more or less transparent appearance to an opaque one, due to the great development of the fat-body.

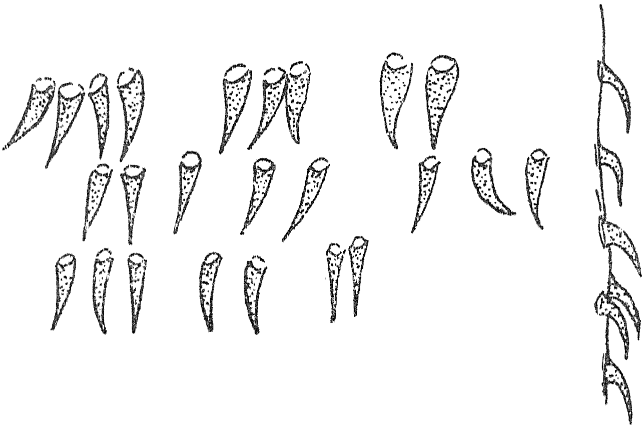
Great difficulty was experienced in determining whether the whole of the chitinised mouth-parts were thrown off at ecdysis. Owing to the thin epidermis and the impossibility of finding cast skins in the dung, a set of old mouth-parts was never found. Theoretically the complete set should be thrown off, and recently I had the good fortune to mount a preparation within an hour or so of the first moult showing a complete second set outside the old set. Up to this time I had proof that the buccal and

Text-figure 11.



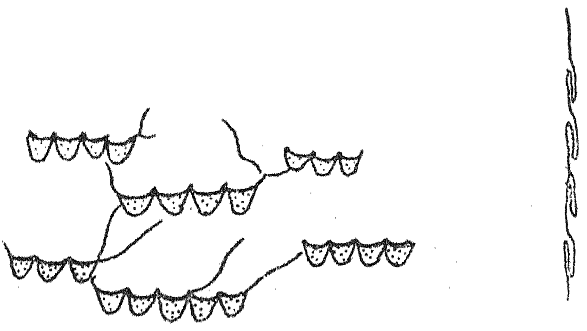
Schematic drawing of anal plate.

Text-figure 12.



Spines of fifth and later segments.

Text-figure 13.



Modified spines of anterior four segments.

intermediary sclerites were thrown off, but it seemed impossible that the larva could be capable of throwing off the large lateral pharyngeal plates. No conclusive proof was obtained of the complete throwing-off of the second instar mouth-parts at the second moult, but this may be taken for granted as occurring as well as at the first moult.

The total larval life takes from 9 to 12 days. The minimum time observed was 8 days and the maximum 14 days. Eleven days is the usual length of time under laboratory conditions.

The total larval life and the ultimate size of the larva, and therefore the puparium, are controlled to a very large extent by the temperature and condition of the breeding medium. Lack of moisture is a very important factor. This explains the variety in size of the adults.

The Puparium.

At pupation the two anterior segments of the larva are withdrawn, bringing the anterior spiracles in a forward position. In this position the larval skin slowly changes to the brick-red colour characteristic of the puparium (text-fig. 14). The colour changes to black as the pupal period advances. It is more or less cigar-shaped; the anterior end is slightly flattened dorsoventrally. The anterior spiracles can be seen as two dark projections at the anterior end. It measures from 6 mm. to over a centimetre in length. The size varies according to the conditions governing the life of the larva, mentioned earlier.

From larvæ bred in the laboratory a large percentage pupated in the hardened upper crust of the dung. This was probably due to the soil being too moist in the jars, as there was no outlet to allow the excess moisture to get away. Under ordinary conditions the soil is preferred, as in field observations very few puparia were observed in dung.

The pupal period takes from 10 to 17 days. The minimum time observed was 6 days and the maximum 18 days.

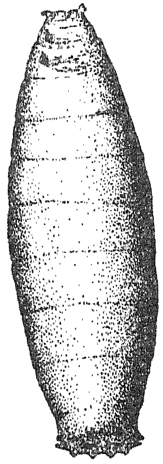
The following data give the comparative larval and pupal periods for a number of batches bred:—

Oviposition.	Egg.	I. instar	II. instar.	III. instar.	Pupa.	Total.	Emergence.
Jan. 5th.	48–54 hrs.	36 hrs.	36–60 hrs.	6-7 days.	6 days.	17-19 days.	Jan. 22-24.
Feb. 17th.	20–24 hrs.	36 hrs.	60 hrs.	6 days.	13-14 days.	24-25 days.	Mar. 12-13.
Mar. 1st.	36–42 hrs.	36 hrs.	36 hrs.	6-7 days.	9–10 days.	19-21 days.	Mar. 20-22.
Mar. 18th.	48 hrs.	36 hrs.	36 hrs.	9 days.	16-17 days.	30-31 days.	Apr. 17-18.
May 7th.	48 hrs.	36 hrs.	48 hrs.	7–8 days.	16 days.	28-30 days.	June 4-6.

The minimum time from adult to adult observed was 17 days and the maximum 31 days. The average time from the table given above is 24 days, but this time, as stated earlier, is governed by temperature and the consistency of breeding media.

In one batch of larvæ bred in dry dung the larvæ were observed to have collected in one spot where the only moisture was. These did not reach the third instar until after a week of larval life. They were transferred to fresh dung later, so that the total larval life was not observed. Under similar conditions the larval life may take as much as three times as long as the maximum observed.

Text-figure 14.



Puparium.

Sexual maturity is not reached until after 21 days of adult life. During this time the males have no attraction towards the females, and, owing to the male being the more robust, the latter are liable to be attacked unless a sufficient supply of food is maintained.

Copulation takes place about two days before oviposition. The life of the male is considerably longer than that of the female. No definite results were obtained on the life of the female. No females were observed to lay more than 120 eggs. It is probable that one female is capable of laying from 100 to 150 eggs and then dies. Eggs are laid in one batch of from 40 to 80 and afterwards, 10 or 20 at a time at intervals.

The total life-cycle from egg to egg takes from six to seven weeks.

Breeding takes place regularly from April to October, and there are probably five broods a year.

No definite results were obtained on hibernation, but evidently a large number hibernate as adults. A number of pupæ were exposed to cold weather during December, but the adults all emerged without exception. This implies that hibernation does not take place in the pupal stage, but it may be that the process of histogenesis had proceeded beyond a certain point before being placed in the cold, and the breaking down and building up of tissues in the pupæ were carried on. A large amount of adults are seen about on warm sunny days in winter, but 90 per cent. are males. I think that probably the majority hibernate as adults, but that only those females survive that failed to oviposit before the cold weather set in. This would account for the difference in proportion of the sexes. Probably a few survive the winter as puparia and the larger proportion as adults. Investigations extended over another winter would prove this point. Graham-Smith remarks that *S. stercoraria* hibernates as a resting larva or pupa in the soil, a few surviving the winter as adults.

A number of flies were placed in a glass-house heated by two electric radiators. During one night the temperature rose to over 90° F., with the result that they were all found dead the following morning. It appears from this that the fly is not capable of withstanding high temperatures. The fly is, however, a subtropical one as well as a temperate one, and should therefore be able to stand this temperature. The sudden change from a mild temperature to a hot one and the lack of ventilation were probably the cause. It must also be remarked that the flies were of a very large variety. The largest and smallest varieties are not so resistant to unfavourable conditions as the average sized varieties.

The food of the adults is very varied, but confined to other Diptera. The small Borborid fly (*Borborus equinus*) appears to be the chief article of diet in the field, chiefly as it breeds abundantly in horse excrement and as it passes the winter as an adult. Larger flies, however, are preyed upon, such as *Calliphora*, *Lucilia*, *M. domestica*, etc. Probably all species of Diptera are preyed upon, with the exception of those of fast flight, such as Syrphidæ and Stratiomyidæ. I observed, on one occasion, a large male attempt to capture a small dung-beetle (*Geotrupes*) as the latter was settling. At the Zoological Gardens in 1915 Professor Lefroy's experiments with fly-traps were interfered with by the abundance of the adult *S. stercoraria* that fed on the trapped flies, chiefly blow-flies of the genus *Calliphora*.

In summer the adults may be seen on plants and flowers far away from pastures waiting for other flies to settle in the vicinity.

M. domestica was used as food almost entirely in the laboratory, each fly sucking out as many as a dozen a day.

Natural Enemies.

Natural enemies were not observed. The Scarabeid and Staphylinid beetles and their larvae, which breed in dung, do not appear to attack the larvæ of *Scatophaga*.

One Ichneumonid parasite was bred out from pupæ, but, having failed to reach the surface of the soil, was in too bad a state of preservation to be identified.

A large number of birds are mentioned by Newstead as feeding on Scarabeid beetles and Muscid larvæ breeding in dung, so that they very probably are a considerable check on the spread of *Scatophaga*.

A number of larvæ are probably destroyed by natural conditions such as the too rapid drying up of the dung or owing to the dung being trodden on and spread about by cattle.

Bibliography.

1. Becker, T.—Dipterologische Studien. I. Scatomyzidæ. Berlin. Ent. Zeit. 1894, pp. 77–190.
2. Becker & Bezzi.—Katalog der Paläarktischen Dipteren.
3. Graham-Smith, G. S.—Flies in Relation to Disease: non-blood-sucking flies. Cambridge (Public Health Series), 1913. (Pp. xiv+292.) 24 pls.
4. —— Observations on the Habits and Parasites of Common Flies. Parasitology, viii. (1915–16), pp. 441–547.
5. Hewitt, C. G.—The House-Fly.—Biological Series, No. 1. Manchester University Press.
6. —— Journal of Economic Biology, 1907.
7. —— Canadian Entomologist, xlvi. (1914), p. 2.
8. Keilin, D.—Recherches sur les Anthomyides à Larves Carnivores. Parasitology, ix. (1916–17).
9. Lowne, B. T.—The Anatomy, Physiology, Morphology, and Development of the Blow-fly. Vols. I. & II.
10. Mellor, J. E. M.—Observations on the Habits of certain Flies. Annals of Applied Biology, vol. vi. (Sept. 1919).
11. Newstead, R.—The Food of some British Birds. Journ. of the Board of Agriculture, vol. xv. No. 9 (Dec. 1908).
12. Patton & Cragg.—Text-book of Medical Entomology.
13. Poulton, E. B.—Predaceous Insects and their Prey. Proceedings of the Entomological Society, 1906.
14. Williston, S. W.—Manual of North American Diptera. (1908.) James F. Hathaway, New Haven.

35. Remarks on the Respiratory Movements of *Necturus* and *Cryptobranchus*. By A. Willey, M.A., D.Sc., F.R.S., F.Z.S.

[Received October 25, 1920: Read November 2, 1920.]

In a former paper certain facts were published showing that, under the conditions of observation, *Necturus*, the "Mud Puppy" or "Gilled Salamander," is normally a water-breather, not an air breather*. Shortly afterwards I had the opportunity (May 24 and 25, 1918) of observing *Necturus* under the conditions presented to it in the New York Aquarium, and of comparing its behaviour with that of the "hellbender," *Cryptobranchus* [= *Menopoma*].

Between 11 A.M. and noon on May 24, after watching for ten minutes, I saw one *Cryptobranchus* yawn slowly to the full extent of its gape under water at the bottom of the deep aquarium. Two others afterwards went through the same performance, *i. e.* yawning under water. There were more than a dozen individuals, all resting at the bottom of the aquarium during my forty-minute vigil. One of them gave two rather copious emissions of air from the mouth, and a bubble was seen to rise from the right gill-pore. None visited the surface. While at the bottom they have a way of swaying gently from side to side, whereby the longitudinal lateral cutaneous flap waves up and down.

At the same hour on the following day I found the hellbenders actively engaged in ascending to the surface, remaining for some minutes just below the surface suspended in the water with arched back, retaining that attitude whilst sinking to the bottom, or else deliberately swimming to the bottom. They protruded their muzzles above the surface without opening the mouth, and in one case a deep inspiration through the nostrils was effected by the dilatation of the hyobranchial apparatus. The air thus taken in may be expelled quickly from the mouth in a continuous stream of bubbles, perhaps indicating that it had been used for oropharyngeal respiration.

Giant Salamanders (*C. maximus*), in a neighbouring tank, behaved like the hellbenders. On May 24 they were resting at the bottom of the deep aquarium; one of them emitted some air through the mouth; none visited the surface. But on the following day they were restless, ascending to the surface. I saw one of them, after pushing its muzzle above the surface, take a slow and deep inspiration through the nostrils by the dilatation, to full capacity, of the hyobranchial apparatus. The latter bulges conspicuously downwards and backwards so that the greatest convexity lies behind, at the base of the throat. Presumably, in this act of dilation, the glottis is opened; and, in fact, *Cryptobranchus* seems to show some increase of girth after inhalation.

---

* A. Willey: "Branchioderma and Branchiotrema." Trans. Roy. Soc. Canada, 3rd ser. vol. xii. sect. iv. (May 1918), pp. 95–104. Ottawa, 1919.

Inhalation through the nostrils was observed by G. B. Wilder in a Japanese *Cryptobranchus*, 2½ feet long, which he kept in shallow water sufficient to cover it *. The downward protrusion of the floor of the mouth in narial inspiration, the arching of the back, and the swaying movement at the bottom have been described by A. M. Reese †, who adds that the hellbender will survive more than a week's exposure out of water without suffering any peramanent diminution of vitality. The longest time that any individual was observed by him to remain under water was 43 minutes. B. G. Smith ‡ confirmed the observation that the arching of the back is a sign that air has entered the lungs. No writer seems to have reported the extraordinary yawning under water to which I have alluded.

Another equally deep tank held at least a dozen examples of *Necturus*. On both occasions they remained undisturbed at the bottom of the aquarium without betraying any signs of unusual activity such as would attend recent or approaching visits to the surface. Some of them had lived for three years in the aquarium; their bodies were sleek, firmly rounded, and fully extended.

There is a point concerning the vascular system which requires slight emendation. All the blood that leaves the heart of *Necturus* passes through the afferent branchial arteries to the external gills. J. E. V. Boas (Morph. Jahrb. vii. 1882) had described an external carotid artery arising from the first afferent artery on each side, between the heart and the base of the first gill. I have satisfied myself by injection that this artery does not exist in the position claimed for it by Boas. It arises from the first efferent artery as described and figured by W. S. Miller §.

Unfortunately, two papers by H. L. Bruner had escaped my notice earlier ‖. In these regular oscillations of the floor of the mouth in aquatic respiration are attributed to *Necturus*, and, under certain experimental conditions, of which temperature is one of the factors, pulmonary respiration is stated to occur at intervals. Bruner's analysis of the respiratory movements observed by him in *Necturus* does not include the gross flapping of the external gills. There is, therefore, an apparent textual discrepancy between his account and mine, which will doubtless be cleared by further independent observations. Bruner fortifies his statements concerning the "bucco-pharyngeal mechanism" by a careful description of the choanal valve of *Necturus*; and he seems to assign a preponderating rôle to the gill-clefts in the branchial respiration of this genus. It is not altogether inconceivable that in different parts of its climatic range, as well as under diverse laboratory conditions, the several components of the respiratory tract may vary in the relative frequency of their turns. The behaviour of *Cryptobranchus* informs us that not every yawn is an act of breathing. No contrast could be more realistic than that between the restless, air-craving *Cryptobranchus* and the listless, gill-waving *Necturus* when viewed at the right biological moment in the splendidly appointed tanks of the New York Aquarium.

---

* Burt G. Wilder: "On the habits of *Cryptobranchus*." Amer. Nat. xvi. pp. 816-817, 1882.

† Albert M. Reese: "The habits of the Giant Salamander." Pop. Science Monthly, vol. lxii. pp. 526-531. New York, 1903.

‡ Bertram G. Smith: "The life-history and habits of *Cryptobranchus alleghaniensis*." Biol. Bull. xiii. pp. 5-39, 1907.

§ W. S. Miller: "The vascular system of *Necturus maculatus*." Contributions from the Anatomical Laboratory of the University of Wisconsin, Bull. Univ. Wisconsin, No. 33, Science Series, vol. ii. No. 3, pp. 211-226, pls. ix.-xi. Madison, Wisconsin, 1900.

‖ H. L. Bruner: 1. "The Mechanism of Pulmonary Respiration in Amphibians with Gill-Clefts." Morph. Jahrb. xlviii. pp. 63-82, 1914. 2. "Jacobson's Organ and the Respiratory Mechanism of Amphibians." *Ibid.* pp. 157-165.

McGill University, Montreal,
October 10, 1920.

EXHIBITIONS AND NOTICES.

October 19th, 1920.

Prof. E. W. MacBride, F.R.S., F.Z.S., Vice-President, in the Chair.

The Secretary read the following Report on the Additions to the Society's Menagerie during the months of June, July, August, and September, 1920.

June.

The registered additions to the Society's Menagerie during the month of June were 495 in number. Of these 267 were acquired by presentation, 32 were deposited, 155 were purchased, 12 were received in exchange, and 29 were born in the Menagerie.

The following may be specially mentioned:—

Mammalia.

1 American Bison (*Bison americanus*), ♂, born in the Menagerie on June 1st.

1 Duke of Bedford's Deer (*Cervus xanthopygius*), ♀, from Manchuria, deposited by H.G. The Duke of Bedford, K.G., Pres. Z.S., on June 2nd.

1 Hippopotamus (*Hippopotamus amphibius*), ♀, from the Upper Nile, purchased on June 9th.

1 Oak-Dormouse (*Dyromys nitidula*), from Kedos, Anatolia, presented by Capt. G. Noel Rogers on June 5th. New to the Collection.

Aves.

1 Grey-cheeked Thrush (*Hylocichla aliciæ*), from N. America; 1 Red-eyed Vireo (*Vireo olivacea*), from N. America; 2 Californian Ground-Finches (*Pipilo crissalis*), from N. America; 2 Texas Colins (*Colinus texanus*), from Texas; 4 Mexican Goldfinches (*Chrysomitris mexicanus*), from Mexico; 4 Pine-Siskins (*Spinus pinus*), from N. America; 2 Rufous-winged Tyrants (*Pitangus rufipennis*), from Colombia; 1 San-blas Jay (*Cissolopha sanblasiana*), from Mexico; 2 Inca Doves (*Scardafella inca*), from Central America; 1 Venezuelan Motmot (*Momotus venezuelæ*), from Venezuela; 2 Red-winged Doves (*Chamæpelia rufipennis*), from Central America; 2 Mexican Ground-Doves (*Chamæpelia pallescens*), from Mexico; 1 Northern Guan (*Ortalis maccalli*), from S. Texas; 1 Western Gull (*Larus occidentalis*), from Pacific Coast of N. America; 1 Pacific Gull (*Gabianus pacificus*). All presented by the Zoological Society of New York on July 9th, and all new to the Collection.

3 Burchell's Glossy Starlings (*Lamprocolius australis*), from S. Africa, received in exchange on June 17th. New to the Collection.

Reptilia.

1 Night Tree-Snake (*Dipsadomorphus dendrophilus*), from Malay Peninsula, purchased June 4th. New to the Collection.

JULY.

The registered additions to the Society's Menagerie during the month of July were 413 in number. Of these 71 were acquired by presentation, 24 were deposited, 231 were purchased, and 87 were born in the Menagerie.

The following may be specially mentioned:—

Mammalia.

2 Tigers (*Felis tigris*), from India, presented by The Maharajah of Ratlam on July 16th.

1 Indian Elephant (*Elephas maximus*), from India, presented by The Maharajah of Cooch Behar, K.C.S.I.

Aves.

2 Yellow-collared Macaws (*Ara auricapilla*), from Eastern Bolivia, presented by Walter Goodfellow, F.Z.S., on July 23rd. New to the Collection.

5 Northern Boatbills (*Cancroma zeledoni*), from Mexico, purchased on July 9th.

Reptilia, Batrachia, Pisces.

2 Indian Cobras (*Naia tripudians*), 1 Hamadryad (*Naia bungarus*), 2 Russell's Vipers (*Vipera russelli*), and 1 Banded Krait (*Bungarus fasciatus*), from India; purchased on July 16th.

AUGUST.

The registered additions to the Society's Menagerie during the month of August were 144 in number. Of these 37 were acquired by presentation, 73 were deposited, 24 were purchased, 8 were received in exchange, and 2 were born in the Menagerie.

The following may be specially mentioned:—

2 Black-and-White Guerezas (*Colobus abyssinicus*), from the Lotuka District, Mongalla Province, S. Soudan, presented by Capt. W. R. Barker on August 1st.

2 Leopards (*Felis pardus*) and 1 Baboon (*Papio anubis*), from Southern Nigeria, presented by A. E. F. Murray on August 19th.

2 Boddaert's Squirrels (*Callosciurus notatus*), from Java, purchased on August 12th.

2 Collared Sunbirds (*Anthothreptes collaris*), new to the Collection, from Natal, presented by Harold Millar on August 2nd.

2 Brazilian Cariamas (*Cariama cristata*), from Morro Velho, Brazil, presented by George Chalmers, C.M.Z.S.

2 Daudin's Vipers (*Vipera lebetina*), new to the Collection, from Algeria, deposited on August 19th.

SEPTEMBER.

The registered additions to the Society's Menagerie during the month of September were 158 in number. Of these 105 were acquired by presentation, 28 were deposited, 9 were purchased, 4 were received in exchange, and 12 were born in the Menagerie.

The following may be specially mentioned:—

3 Polar Bears (*Thalarctos maritimus*), ♂ ♀ ♀, from Greenland, purchased on September 1st.

1 Bosman's Potto (*Perodicticus potto*), from Ashanti, presented by Mrs. Beddington on September 22nd.

1 Kaffir Mongoose (*Mongos caffer*), from Ikirun, S. Nigeria, new to the Collection, presented by R. H. Lapage, Esq.

1 Banded Squirrel (*Callosciurus vittatus*), from N. Borneo, new to the Collection, deposited on September 23rd.

1 Green-headed Amazon (*Chrysotis virenticeps*), from Central America, received in exchange on September 30th. New to the Collection.

Dr. P. Chalmers Mitchell, F.R.S., F.Z.S., exhibited a Double tailed Lizard, and illustrated his remarks with a series of radiographs and lantern-slides.

November 2nd, 1920.

Sir Sidney F. Harmer, K.B.E., F.R.S., Vice President, in the Chair.

Mr. R. I. Pocock, F.R.S., F.Z.S., exhibited, on behalf of Mr. E. Gerrard, the skin of the groin of an example of *Tragelaphus buxtoni*, proving the presence of inguinal glands in that Antelope.

Mr. E. G. Boulenger, F.Z.S., exhibited, and made remarks upon, living specimens of *Necturus*, presented to the Society by Dr. A. Willey, F.R.S., F.Z.S.

Mr. T. A. Barns, F.Z.S., gave an account of his recent expedition through the forests of Africa in search of Gorilla and Okapi, illustrating his remarks with a fine series of cinematograph films.

November 16th, 1920.

Prof. J. P. Hill, D.Sc., F.R.S., Vice-President,
in the Chair.

The Secretary read the following Report on the Additions to the Society's Menagerie during the month of October, 1920:—

The registered additions to the Society's Menagerie during the month of October were 273 in number. Of these 80 were acquired by presentation, 37 were deposited, 151 were purchased, 1 was received in exchange, and 4 were born in the Menagerie.

The following may be specially mentioned:—

1 Maned Wolf (*Canis jubatus*) and a Crab-eating Dog (*Canis thous*), from Morro Velho, Brazil; presented by Mr. George Chalmers, C.M.Z.S., on October 18th.

2 Bay Duikers (*Cephalophus dorsalis*) and 1 Maxwell's Duiker (*C. maxwelli*), from Togoland; presented by Dr. Malcolm B. Hay on October 7th.

A collection of mammals and birds from the East, purchased on October 13th, containing 2 De Brun's Wallabies (*Macropus brunii*), from Aru; 1 Ursine Tree-Kangaroo (*Dendrolagus ursinus*), from Northern New Guinea, and the following birds which are new to the Collection: 1 Sula Island Calornis (*Lamprocorax sulaensis*); 1 Black-headed Butcher-Crow (*Cracticus cassicus*), from Aru; 1 Rosenberg's Lorikeet (*Trichoglossus rosenbergi*), from Mysore; 1 Mueller's Imperial Fruit-Pigeon (*Carpophaga muelleri*), from Aru; 1 Pinon Imperial Fruit-Pigeon (*Carpophaga pinon*) and 2 Finsch's Imperial Fruit-Pigeons (*Carpophaga finschi*), from New Ireland.

Mr. J. T. Cunningham, M.A., F.Z.S., exhibited, and made remarks upon, a specimen of the Leech *Trocheta*, recently found in the Society's Gardens.

Mr. F. Martin Duncan, F.Z.S., exhibited, and made remarks upon, a series of cinematograph films, which he had taken of animals in the Society's Gardens.

INDEX OF ILLUSTRATIONS.

Acanthocheilonema diacantha, Figs. 3, 4, pp. 495, 496.
—— *gracile*, Figs. 5, 6, 7, pp. 497, 498.
African Lakes, Table to illustrate richness of Fauna, Fig. 2, p. 594.
Alopecopsis atavus, Figs. 4, 6, pp. 347, 349, 350.
Alysia manducator, Figs. 1–12, pp. 199, 201–203, 205, 206, 208, 209, 212.
Arthroleptis stenodactylus, Fig. 1, p. 414.

Branchiodrilus hortensis, Figs. 1, 3, pp. 459, 463.
Bufo stomaticus, Fig. 1, p. 445.

Chalicotheroidea, Figs. 5–7, pp. 364, 365.
Copera atomaria, Fig. 4, p. 334.
Curve showing growth of knowledge of Tanganyika fauna, Fig. 1, p. 593.

Diplotriæna diucæ, Figs. 9, 10, pp. 501, 502.
—— *flabellata*, Fig. 11, p. 503.
—— *tricuspis*, Fig. 8, p. 500.

Echinocephalus multidentatus, Pls. VI.–VIII., p. 245; Figs. 33–36, pp. 286, 287, 290.
—— *southwelli*, Pls. IV.–V., p. 245; Figs. 30–32, pp. 282–284.
—— *spinosissimus*, Pl. IV., p. 245; Figs. 25–29, pp. 279–281.
—— *uncinatus*, Fig. 24, p. 276.

Filaria aramidis, Fig. 12, p. 504.
—— *subcutanea*, Figs. 1, 2, pp. 492, 493.
Flying-fish, Flight of, Figs. 1, 2, pp. 469, 473.

Gnathostoma spinigerum, Pls. VII., VIII., p. 245; Figs. 37–40, pp. 293–295.

Ictidosuchus longiceps, Figs. 1–3, pp. 344–346.

Megalixalus loveridgii, Fig. 4, p. 418.
Meles meles, Figs. 19–25, pp. 425, 427, 429, 431, 432, 434, 435.
Melittobia acasta, Fig. 20, p. 240.
Moschorhinus kitchingi, Figs. 7, 8, pp. 351, 353.

Nais pectinata var. *inæqualis*, Figs. 1, 2, pp. 459, 460.
Nasonia brevicornis, Figs. 13–20, pp. 217–220, 222, 225, 226, 240.

Peripatoides, Pls. I.–V., p. 367.
Phyllotillon naricus, Pl. I., p. 357; Figs. 1, 2, pp. 358, 360.
Proleptus scillicola, Figs. 1–3, pp. 451, 452, 454.

Rana holsti, Fig. 5, p. 421.
Rappia platyrhinus, Fig. 3, p. 416.
—— *puncticulata*, Fig. 2, p. 415.

Rhinocypha moultoni, Figs. 1, 2, pp. 329, 330.
Scatophaga stercoraria, Figs. 1–14, pp. 631–645.
Schizotherium ? pilgrimi, Pl. I., p. 357; Figs. 3, 4, pp. 362, 363.
Spiroxys contorta, Pls. I., II., p. 245; Figs. 1–3, p. 250.
—— *gangetica*, Pl. II., p. 245; Figs. 4–6, p. 252.

Tanganyika fauna, Curve showing growth of knowledge of, Fig. 1, p. 593.
Tanqua anomala, Pl. IV., p. 245; Figs. 16–20, pp. 265–267.
—— *diadema*, Pls. III., IV., p. 245; Figs. 21–23, p. 269.
—— *tiara*, Pl. III., p. 245; Figs. 7–15, pp. 259–261, 263, 264.
Taxidea americana, Figs. 19, 20, 22–25, pp. 425, 427, 431, 432, 434, 435.
Teinobasis kirbyi, Fig. 4, p. 337.
Teredo mannii, Figs. 2, 3, pp. 395, 396.
—— *navalis*, Fig. 1, p. 393.

Whaitsia platyceps, Fig. 9, p. 354.

Xylotrya australis, Figs. 6–8, pp. 399–401.
—— *capensis*, Figs. 9–11, pp. 401–403.
—— *sauli*, Figs. 4, 5, p. 399.

INDEX.

1920.—Pages 195–656.

[New names in clarendon type. Systematic references in italics. (z. s. l.) indicates additions to the Society's Menagerie.]

Acanthocephala, 410.
Acanthocheilonema diacantha, 494.
—— *gracile*, 496.
Aciagrion borneense, 336.
Adalia bipunctata, 475.
Æschnidæ, 312.
Æschninæ, 312.
Ætheriidæ, 552.
Æthriamanta gracilis, 325.
Agriocnemis femina, 336.
—— *rubescens*, 336.
Agrion, Legion, 335.
Agrionoptera insignis, 321.
—— *sexlineata*, 321.
Alluroididæ, 574.
Alopecopsis atavus, gen. et sp. nov., 517.
Alysia manducator, 199.
Ammotragus lervia (z. s. l.), 437.
Amphiæschna grubaueri, 314.
—— *perampla*, 314.
Amphicnemis louisæ, 336.
—— *madelenæ*, 336.
—— *martini*, 336.
—— *remiger*, 336.
—— *wallacei*, 336.
Ampullariidæ, 543.
Anabantidæ, 529.
Anaciæschna jaspidea, 316.
Anastillorhina augur, 230.
Anax guttatus, 316.
Ancylidæ, 545.
Ancyracanthus, 305.
Anisoptera, 312.
Ara auricapilla (z. s. l.), 654.
Argulus incisis, 564.
Arthroleptis minutus, 414.
—— *stenodactylus*, 414.
—— *wahlbergii*, 414.
—— *whytii*, 414.
Anthropopithecus troglodytes (z. s. l.) 437.
Anthrothreptes collaris (z. s. l.), 654.
Ascaris sphærocephala, 271.
Atyidæ, 555.
Azuma australis, 317.
—— *vittigera*, 318.

Bdelloida, 580.
Bison americanus (z. s. l.), 655.
Bosminidæ, 568.
Boulengerina stormsi, 520.
Brachydiplax chalybea chalybea, 322.
Brachygonia oculata, 322.
—— *ophelia*, 322.

Brachyura, 556.
Branchiodrilus hortensis, 463.
Branchiopoda, 571.
Branchiura, 563.
Breviceps mossambicus, 420.
Bubo cavens, 420.
—— *lacteus* (z. s. l.), 437.
Bufo regularis, 420.
—— *stomaticus*, 441.
Bungarus fasciatus (z. s. l.), 654.
Burmagomphus vermiculatus, 317.

Caconeura collaris, 339.
—— *dorsalis*, 339.
—— *gracillima*, 340.
—— *hosei*, 339.
—— *hyperythra*, 339.
—— *interrupta*, 339.
—— *lansbergi*, 339.
—— *moultoni*, 340.
—— *peramœna*, 339.
—— *verticalis*, 339.
Calliphora erythrocephala, 196, 198, 230.
—— *vomitoria*, 198.
Callosciurus notatus (z. s. l.), 654.
—— *vittatus* (z. s. l.), 655.
Calopteryginæ, 325.
Camacinia harterti, 325.
Cancroma zeledoni (z. s. l.), 654.
Canis jubatus (z. s. l.), 656.
—— *thous* (z. s. l.), 656.
Cariama cristata (z. s. l.), 655.
Carpophaga finschi (z. s. l.), 656.
—— *muelleri* (z. s. l.), 656.
—— *pinon* (z. s. l.), 656.
Cassina senegalensis, 419.
Centropagidæ, 559.
Cephalophus dorsalis (z. s. l.), 656.
—— *maxwelli* (z. s. l.), 656.
Ceriagrion bellona, 335.
—— *cerinorubellum*, 335.
Cervus xanthopygius (z. s. l.), 653.
Cestoda, 408, 585.
Chætonotus formosus, 582.
—— *pusillus*, 582.
Chamæpelia pallescens (z. s. l.), 653.
Chamæpelia rufipennis (z. s. l.), 653.
Characidæ, 521.
Chiromantis petersi, 413.
—— *xerampelina*, 413.
Chlorogomphinæ, 312.
Chonopeltis inermis, 564.
Chrysomia macellaria, 230.
Chrysomitris mexicanus (z. s. l.), 653.
Chrysotis viridiceps (z. s. l.), 655.
Chydoridæ, 568.
Cichlidæ, 526.
Ciliata, 590.
Cissolopha sanblasiana (z. s. l.), 653.
Cladocera, 567.
Clarotes laticeps, 438.
Clupeidæ, 524.
Coccinella variabilis, 487.
Cœlenterata, 585.
Cœliccia borneensis, 334.
—— *campioni*, 333.
—— *flavostriata*, 333.
—— *macrostigma*, 333.
—— *membranipes*, 333.
—— *nigrohamata*, 333.
—— *octogesima*, 333.
Colinus texanus (z. s. l.), 653.
Colobus abyssinicus (z. s. l.), 654.
Connochætes albojubatus, 437.
Copera atomaria, 334.
Corduliinæ, 317.
Cracticus cassicus (z. s. l.), 656.
Cratilla lineata, 321.
—— *metallica*, 321.
Crioceris asparagi, 486.
Crocodilus cataphractus, 519.
—— *niloticus*, 519.
—— *siamensis* (z. s. l.), 439.
Crocothemis servilia, 325.
Cryptobranchus, 649.
Cycloderma frenatum, 521.
Cyclopidæ, 560.
Cynælurus jubatus (z. s. l.), 438.
Cynomyia cadaverina, 230.
Cypridæ, 565.
Cyprinidæ, 525.
Cyprinodontidæ, 526.
Cyrenidæ, 551.
Cytheridæ, 565.

Daphnidæ, 567.
Dendrolagus ursinus (Z. S. L.), 656.
Deradutta argyroides, 332.
Dicheilonema horridum, 499.
Diplacodes trivialis, 323.
Diplotriæna diucæ, sp. n., 501.
—— *flabellata*, 502.
—— *tricuspis*, 499.
Dipsadomorphus dendrophilus (Z. S. L.), 654.
Disparoneura analis, 340.
—— *aurantiaca*, 340.
Dolops ranarum, 564.
Dorylaimus macrolaimus, 577.
Drepanosticta rufostigma, 340.
Dyromys nitidula (Z. S. L.), 653.
Dysphæa limbata, 327.
—— *lugens*, 327.

Echinocephalus, 273, 275.
—— **multidentatus**, sp. n., 285, 288, 289.
—— **southwelli**, sp. n., 283, 285, 288.
—— *spinosissimus*, 277, 283, 288.
—— *striatus*, 289.
—— *uncinatus*, 275, 277, 288.
Elaphocephalus, 306.
Elephas maximus (Z. S. L.), 654.
Epallaginæ, 326.
Ergasilidæ, 560.
Eucopepoda, 559.

Felis tigris (Z. S. L.), 654.
Filaria aramidis, sp. n., 503.
—— *subcutanea*, 492.
Flying-Fishes, 467.
Francolinus spilogaster (Z. S. L.), 439.

Gabianus pacificus (Z. S. L.), 653.
Gastrotricha, 581.
Glossoscolecidæ, 574.
Glypholycus bicolor, 520.
Gnathostoma, 291, 292.
—— *accipitri*, 305.
—— *gracile*, 300, 301, 303, 304.
—— *hispidum*, 298, 300, 303, 304.
Gnathostoma horridum, 300, 303, 304.
—— *pelecani*, 301.
—— *shipleyi*, 301.
—— *spinigerum*, 293, 298, 302, 304.
—— *turgidum*, 301, 303, 304.
Gnathostomidæ, 245.
Gnathostominæ, 255, 256.
Gomphidia karschi, 317.
—— *maclachlani*, 317.
Gomphinæ, 317.
Gossea pauciseta, 582.
Grayia ornata, 520.
—— *tholloni*, 520.
Gymnolæmata, 539.
Gynacantha basiguttata, 315.
—— *bayadera*, 316.
—— *demeter*, 315.
—— *dohrni*, 315.
—— *hyalina*, 316.
—— *mach'achlani*, 316.
Gyrator hermaphroditus, 584.

Harpacticidæ, 559.
Heliæschna crassa, 313.
—— *idæ*, 313.
—— *simplicia*, 314.
—— *uninervulata*, 314.
Hemicordulia assimilis, 317.
Hemistoma (*Alaria*) *alatum*, 438.
Hemisus marmoratum, 420.
Herpeton tentaculatum (Z. S. L.), 439.
Heterogomphus icterops, 317.
—— *sumatranus*, 317.
Hippopotamus amphibius (Z. S. L.), 653.
Hirudinea, 575.
Hydrachnida, 572.
Hydrobasileus croceus, 324.
Hydrobiidæ, 543.
Hydrochærus hydrochærus (Z. S. L.), 438.
Hydrophantidæ, 572.
Hygrobatidæ, 572.
Hylæothemis clementia, 320.
Hylambates bocagii, 419.
—— *johnstoni*, 420.
Hylobates lar (Z. S. L.), 437.
Hylocichla aliciæ (Z. S. L.), 653.
Hypotænidia striata (Z. S. L.), 437.

Ichthydium macrurum, 582.
Ictidosuchus longiceps, sp. n., 343.
Ictinus acutus, 317.
—— *decoratus*, 317.
—— *melænops*, 317.
Idionyx dohrni, 319.

Jagoria buhri, 313.
—— *modiglianii*, 312.
—— *pœciloptera*, 313.

Lamprocolius australis (z. s. l.), 653.
Lamprocorax sulaensis (z. s. l.), 656.
Larus occidentalis (z. s. l.), 653.
Lathrecista asiatica, 321.
Lepidoderma hystrix, 582.
—— *squamatum*, 582.
Lepidosirenidæ, 524.
Leptogomphus semperi, 317.
—— *williamsoni*, 317.
Lernæidæ, 560.
Lestes wallacei, 340.
Libellaginæ, 328.
Libellulidæ, 317.
Libellulinæ, 319.
Limnæidæ, 545.
Linæschna polli, 312.
Lucilia cæsar, 198, 230.
—— *sericata*, 198, 230.
Lybius torquatus (z. s. l.), 439.
Lyriothemis biappendiculata, 320.
—— *cleis*, 320.

Mabuia quinquetæniata (z. s. l.), 437.
Macrogomphus albardæ, 317.
—— *chelifer*, 317.
—— *decemlineatus*, 317.
—— *quadratus*, 317.
Macromia borneensis, 318.
—— *cincta*, 318.
—— *cingulata*, 318.
—— *euterpe*, 318.
—— *gerstæckeri*, 318.
—— *westwoodi*, 318.
Macromidia fulva, 319.
Macropus brunii (z. s. l.), 656.
Macrothricidæ, 568.
Macrura, 561.
Mactra adelaidæ, 529.
Malacopleura, 589.
Matronoides cyaneipennis, 326.
Megalocolus lowrangii, 418.
Megapodagrion, Legion, 332.
Megascolecidæ, 571.
Meles, 423, 433.
Melittobia acasta, 231.
Metaphya micans, 319.
Micromerus aurantiacus, 331.
—— *hyalinus*, 332.
—— *semiopacus*, 331.
—— *stictieus*, 332.
Momotus venezuelæ (z. s. l.), 653.
Mungos caffer (z. s. l.), 655.
Monhystera fülleborni, 477.
—— *similis*, 577.
—— *vulgaris*, 577.
Mononchus macrostoma, 577.
—— *tenuis*, 577.
Monostoma pumilo, 458.
Mormyridæ, 524.
Moropus elatus, 357, 359.
Moschorhinus kitchingi, gen. et sp. nov., 351.
Musca domestica, 198, 230.
Mutelidæ, 552.

Naia bungarus (z. s. l.), 654.
—— *tripudians* (z. s. l.), 654.
Naidomorpha, 574.
Nais pectinata var. *inæquale*, 458.
Nannophya pygmæa, 322.
Nasonia brevicornis, 216.
Necturus, 649.
Nemathelmia, 405.
Nematoda, 408, 576.
Nesoxenia lineata, 320.
Neurobasis chinensis, 325.
Neurothemis disparilis, 323.
—— *fluctuans*, 323.
—— *terminata*, 323.

Oda dohrni, 320.
Oligochæta, 573.
Onychargia atrocyana, 335.

Onychothemis culminicola celebensis, 324.
—— *culminicola culminicola*, 324.
Orchithemis pruinans, 320.
—— *pulcherrima*, 320.
—— *xanthosoma*, 320.
Orogomphus dyak, 312.
—— *splendidus*, 312.
Ortalis maccalli (Z. S. L.), 653.
Orthetrum chrysis, 322.
—— *glaucum*, 321.
—— *pruinosum clelia*, 321.
—— *sabina*, 321.
—— *testaceum*, 322.
Oryx leucoryx (Z. S. L.), 438.
Ostracoda, 561.

Palæmonidæ, 555.
Pantala flavescens, 325.
Papio anubis (Z. S. L.), 654.
Pelomedusa galeata, 521.
Pentastomida, 571.
Pericnemis stictica, 337.
Peripatoides gilesii, 367.
—— *leuckarti* var. *occidentalis*, 367.
—— *occidentalis*, 367.
—— *woodwardi*, 367.
Peripatus, 367.
Perodicticus potto (Z. S. L.), 655.
Phormia grœnlandica, 198.
—— *regina*, 230.
Phrynobatrachus boulengeri, 413.
—— *natalensis*, 413.
—— *ranoides*, 413.
Phrynomantis bifasciata, 420.
Phylactolæmata, 539.
Phyllotillon naricus, 557.
Pipilo crissalis (Z. S. L.), 653.
Pitangus rufipennis (Z. S. L.), 653.
Planaria tanganyikæ, 583.
Planorbidæ, 545.
Platycnemis, Legion, 333.
Platyhelmia, 405.
Platysticta, Legion, 340.
Ploima, 578.
Podolestes chrysopus, 332.
—— *orientalis*, 332.
Pollenia stygia, 230.
Polypteridæ, 521.
Porifera, 586.
Pornothemis serrata, 320.
Potamarcha obscura, 321.
Potamonidæ, 557.
Proleptus scillicola, 449.
Protoneura, Legion, 338.
Protosticta kinabaluensis, 340.
—— *versicolor*, 340.
Protozoa, 588, 589.
Pseudagrion microcephalum, 335.
—— *pruinosum*, 335.
Pseudagrionoptera diotima, 323.
Pseudophæa basalis, 326.
—— *impar inæquipar*, 327.
—— *subcostalis*, 326.
—— *subnodalis*, 326.
—— *tricolor*, 326.
Pycnosoma rufifacies, 230.
—— *varipes*, 230.
Physaloptera constricta, 272.

Rana delalandii, 412.
—— *holsti*, 421.
—— *mascareniensis*, 412.
—— *nutti*, 412.
—— *ornata*, 413.
—— *oxyrhynchus*, 412.
Raphismia inermis, 323.
Rappia argus, 417.
—— *cinctiventris*, 417.
—— *fulvovittata*, 417.
—— *granulata*, 415.
—— *marmorata*, 417.
—— **platyrhinus**, sp. n., 416.
—— *punctiulata*, 415.
Rhinagrion borneense, 332.
—— *elopura*, 333.
Rhea americana (Z. S. L.), 439.
Rhinochetus jubatus (Z. S. L.), 439.
Rhinoneura villosipes, 331.
Rhizopoda, 589.
Rhizota, 580.
Rhyothemis aterrima, 324.
—— *obsolescens*, 325.
—— *pygmæa*, 324.
—— *phyllis phyllis*, 324.
—— *rufa*, 323.
—— *triangularis*, 325.
Rhinocypha biseriata, 328.

Rhinocypha cucullata, 329.
—— *eximia*, 329.
—— *humeralis*, 329.
—— *karschi*, 328.
—— *moultoni*, 328.
—— *stygia*, 328.
——, sp. A, 329.
——, sp. B, 330.
Rotifera, 578.

Sarcophaga aurifrons, 230.
Scardafella inca (z. s. l.), 653.
Scatophaga stercoraria, 629.
Schilbe mystus, 438.
Schizotherium pilgrimi, sp. n., 362.
Scyllium canicula, 449.
Serranidæ, 526.
Sididæ, 567.
Sieboldius japonicus, 317.
Siluridæ, 525.
Spelerpes fuscus, 437.
Sphæriidæ, 551.
Spinus pinus (z. s. l.), 653.
Spiroxyinæ, subfam. n., 247.
Spiroxys, 248.
—— *contorta*, 249, 251.
—— **gangetica**, sp. n., 251, 253.
Spongillidæ, 587.
Stenagrion dubium, 338.
Stenostoma gileum, 583.
—— *leucops*, 583.
—— *stuhlmanni*, 583.
Sternothærus derbianus, 521.
—— *nigricans*, 521.
—— *sinuatus*, 521.
Struthio molybdophanes (z. s. l.), 439.

Tanqua, 256, 258.
—— *anomala*, 268.
—— *diadema*, 268, 271.
—— *tiara*, 259, 264.
Tardigrada, 573.
Taxidea, 423, 433.
Teinobasis kirbyi, 337.
—— *rajah*, 338.
Teredo, 392.
—— *mannii*, 395.
—— *navalis*, 392.
—— *norvagica*, 394.
Tetracanthagyna brunnea, 315.
—— *degorsi*, 315.
—— *plagiata*, 314.
—— *waterhousei*, 315.
Tetrathemis flavescens, 319.
—— *irregularis hyalina*, 319.
Thalarctos maritimus (z. s. l.), 655.
Tholymis tillarga, 325.
Tiaridæ, 544.
Tilapia nilotica, 438.
Tiphobiidæ, 541.
Tramea limbata, 324.
Trematoda, 407, 584.
Trichoglossus rosenbergi (z. s. l.), 656.
Trilobus gracilоides, 577.
Trithemis aurora, 323.
—— *festiva*, 324.
Trocheta, 656.
Tropidonotus olivaceus, 520.
Turbellaria, 583.
Turtur decipiens (z. s. l.), 439.
—— *isabellina* (z. s. l.), 439.
—— *roseigriseus* (z. s. l.), 439.
Tyriobapta kukenthali, 322.
—— *laidlawi*, 322.
—— *torrida*, 322.

Unionidæ, 551.
Urolestes melanoleucus (z. s. l.), 439.
Urothemis signata insignata, 325.

Vestalis amœna, 326.
—— *beryllæ*, 326.
Vipera lebetina (z. s. l.), 655.
—— *russelli* (z. s. l.), 654.
Vireo olivacea (z. s. l.), 658.
Viviparidæ, 543.
Vortex quadridens, 581.

Whaitsia platyceps, 354.

Xenopus lævis, 522.
—— *muelleri*, 522.
Xylotrya, 397.
—— **australis**, sp. n., 397.
—— **capensis**, sp. n., 402.

Zygonyx iris, 324.
Zygoptera, 325.
Zyxomma petiolatum, 325.

PRINTED BY TAYLOR AND FRANCIS, RED LION COURT, FLEET STREET.

No. 208.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

October 19th, 1920.

Prof. E. W. MacBride, F.R.S., F.Z.S., Vice-President,
in the Chair.

The Secretary read a Report on the Additions to the Society's Menagerie during the months of June, July, August, and September, 1920.

Dr. P. Chalmers Mitchell, F.R.S., exhibited and made remarks upon a Double-tailed Lizard.

Dr. E. H. Hankin, M.A., communicated his paper "Observations on the Flight of Flying-Fishes."

In the absence of Dr. W. N. F. Woodland, a *résumé* of his paper "On some Results of ligaturing the Anterior Abdominal Vein in the Indian Toad (*Bufo stomaticus*)" was given by Sir S. F. Harmer, F.R.S.

---

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Prof. MAXWELL LEFROY, F.Z.S., communicated a paper by Mr. G. COTTERELL on "The Life History and Habits of the Yellow Dung-Fly: a Blow-Fly Check."

The next Meeting of the Society for Scientific Business will be held on Tuesday, November 2nd, 1920, at 5.30 P.M., when the following communications will be made:—

J. H. LLOYD, M.Sc., F.Z.S.

Some Observations on the Structure and Life-History of the Common Nematode of the Dogfish (*Scyllium canicula*).

Mrs. O. A. MERRITT HAWKES, M.Sc., B.Sc.

Observations on the Life-History, Biology, and Genetics of the Lady-bird Beetle, *Adalia bipunctata* Mulsant.

HARU RAM MEHRA, M.Sc.

On the Sexual Phase in certain Indian Naididae (*Oligochaeta*).

E. A. BARNES.

In the Land of the Gorilla and Okapi.

The following Papers have been received:—

WM. A. CUNNINGTON, M.A., Ph.D., F.Z.S.

The Fauna of the African Lakes: a Study in Comparative Limnology, with special reference to Tanganyika.

HENRY F. CARTER.

Description of the Adult, Larval, and Pupal Stages of a new Mosquito from Lord Howe Island, South Pacific.

C. F. SONNTAG, M.D., Ch.B., F.Z.S.

The Comparative Anatomy of the Tongues of the Mammalia.—II. Fam. Simiidae.

C. L. Boulenger, M.A., D.Sc., F.Z.S.

Filariid Worms from Mammals and Birds in the Society's Gardens, 1914–1915.

Augusta Arnback Christie-Linde.

On the Reproductive Organs of the Ascidian *Kükenthalia borealis* Gottschaldt.

E. Hopkinson, D.S.O., M.A., M.B., F.Z.S.

Records of Birds which have bred in Captivity.

S. Monckton Copeman, M.D., F.R.S.

Note on the Capture of a rare Parasitic Fly, *Hammomyia* (*Hylephila*) *unilineata* Zett, on Primrose Hill.

E. Dukinfield Jones, F.Z.S., F.E.S.

Descriptions of New Moths from South-east Brazil.

D. M. S. Watson.

The Basis of Classification of the Theriodontia.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed, and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary.

Zoological Society of London,
Regent's Park, London, N.W. 8.
October 26th, 1920.

No. 209.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

November 2nd, 1920.

Sir SIDNEY F. HARMER, K.B.E., F.R.S., Vice-President,
in the Chair.

In the absence of Dr. A. WILLEY, F.R.S., F.Z.S., a *résumé* of his communication, "A Note on the Respiratory Movements of *Necturus* and *Cryptobranchus*," was given by Mr. E. G. BOULENGER, F.Z.S., who also exhibited living specimens of *Necturus*, presented to the Society by Dr. Willey.

In the absence of the Author, Mr. J. H. LLOYD, M.Sc., F.Z.S., his paper on "Some Observations on the Structure and Life-History of the Common Nematode of the Dogfish (*Scyllium canicula*)" was taken as read.

In the absence of Mrs. O. A. MERRITT HAWKES, M.Sc., B.Sc., a *résumé* of her paper, "Observations on the Life-History, Biology, and Genetics of the Lady-bird Beetle, *Adalia bipunctata* Mulsant," was given by Mr. F. MARTIN DUNCAN, F.Z.S.

Mr. R. I. POCOCK, F.R.S., F.Z.S., exhibited, on behalf of Mr. E. GERRARD, the skin of the groin of an example of *Tragelaphus burtoni*, proving the presence of inguinal glands in that Antelope.

In the absence of the Author, Prof. HARU RAM MEHRA, M.Sc., his paper, "On the Sexual Phase in certain Indian Naididæ (*Oligochæta*)," was taken as read.

---

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Mr. T. A. Barns, F.Z.S., gave an account of his recent expedition through the forests of Africa in search of Gorilla and Okapi, illustrating his remarks with a fine series of cinematograph films.

The next Meeting of the Society for Scientific Business will be held on Tuesday, November 16th, 1920, at **5.30** P.M., when the following communications will be made:—

The Secretary.

Report on the Additions to the Society's Menagerie during the month of October.

Wm. A. Cunnington, M.A., Ph.D., F.Z.S.

The Fauna of the African Lakes; a Study in Comparative Limnology, with special reference to Tanganyika.

Henry F. Carter.

Descriptions of the Adult, Larval, and Pupal Stages of a new Mosquito from Lord Howe Island, South Pacific.

C. L. Boulenger, M.A., D.Sc., F.Z.S.

Filariid Worms from Mammalia and Birds in the Society's Gardens, 1914–1915.

The following Papers have been received:—

C. F. Sonntag, M.D., Ch.B., F.Z.S.

The Comparative Anatomy of the Tongues of the Mammalia.—II. Family Simiidæ.

Augusta Årnbäck Christie-Linde.

On the Reproductive Organs of the Ascidian *Kükenthalia borealis* Gottschaldt.

S. Monckton Copeman, M.D., F.R.S.

Note on the Capture of a rare Parasitic Fly, *Hammomyia (Hylephila) unilineata* Zett, on Primrose Hill.

E. DUKINFIELD JONES, F.Z.S., F.E.S.

Descriptions of New Moths from South-East Brazil.

D. M. S. WATSON, F.Z.S.

The Basis of Classification of the Theriodontia.

B. P. UVAROVE.

The Geographical Distribution of Orthopterous Insects in the Caucasus and in Western Asia.

Miss JOAN B. PROCTER, F.Z.S.

On the Variation of the Scapula in the *Aglossa* and the *Arcifera*.

E. G. BOULENGER, F.Z.S.

Experiments on Colour-changes of the Spotted Salamander (*Salamandra maculosa*), conducted in the Society's Gardens.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary.

ZOOLOGICAL SOCIETY OF LONDON,
REGENT'S PARK, LONDON, N.W. 8.
November 9th, 1920.

No. 210.

ABSTRACT OF THE PROCEEDINGS

OF THE

ZOOLOGICAL SOCIETY OF LONDON.*

November 16th, 1920.

Prof. J. P. Hill, D.Sc., F.R.S., Vice-President,
in the Chair.

The Secretary read a Report on the Additions to the Society's Menagerie during the month of October 1920.

Mr. F. Martin Duncan, F.R.M.S., F.Z.S., exhibited and made remarks upon a series of cinematograph films, which he had taken of Animals in the Society's Gardens.

Mr. J. T. Cunningham, M.A., F.Z.S., exhibited and made remarks upon a specimen of the Leech *Trocheta*, recently found in the Society's Gardens.

Dr. W. A. Cunnington, M.A., F.Z.S., gave an account of his paper on the "Fauna of the African Lakes, with special reference to Tanganyika." After referring to certain physical and geological features which have a bearing on the subject, the nature of the various animal forms inhabiting the lakes was dealt with. Tanganyika was shown to have a very distinctive fauna, in that:—(1) it includes many more different types than any of the other lakes, (2) an extremely large proportion of them are not found elsewhere, (3) certain forms (notably Gasteropoda) are considered to have a marine-like appearance. The view previously put forward which regarded the lake as the remains of an old Jurassic sea was considered untenable, since many of the types thought to be marine and primitive belong to essentially fresh-water groups and show signs of specialisation. The Jurassic hypothesis proves likewise incompatible with recent geological evidence. After discussing various other theories, it was suggested that Tanganyika probably owes its remarkable organisms to a prolonged period of isolation—coupled, perhaps, with the effect of an increased salinity which isolation would involve.

---

* This Abstract is published by the Society at its offices, Zoological Gardens, Regent's Park, N.W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

In the absence of the Authors, Mr. HENRY F. CARTER's paper on "Descriptions of the Adult, Larval, and Pupal Stages of a new Mosquito from Lord Howe Island, South Pacific," and Prof. C. L. BOULENGER's paper on "Filariid Worms from Mammalia and Birds in the Society's Gardens, 1914–1915," were taken as read.

The next Meeting of the Society for Scientific Business will be held on Tuesday, February 8th, 1921, at **5.30** P.M.

A notice stating the Agenda for that Meeting will be circulated early in February.

The following Papers have been received:—

C. F. SONNTAG, M.D., Ch.B., F.Z.S.

The Comparative Anatomy of the Tongues of the Mammalia.—II. Fam. Simiidæ.

AUGUSTA ÅRNBÄCK CHRISTIE-LINDE.

On the Reproductive Organs of the Ascidian *Kükenthalia borealis* Gottschaldt.

S. Monckton Copeman, M.D., F.R.S.

Note on the Capture of a rare Parasitic Fly, *Hammomyia (Hylephila) unilineata* Zett, on Primrose Hill.

E. Dukinfield Jones, F.Z.S., F.E.S.

Descriptions of New Moths from South-East Brazil.

D. M. S. Watson, F.Z.S.

The Basis of Classification of the Theriodontia.

B. P. Uvarov.

The Geographical Distribution of Orthopterous Insects in the Caucasus and in Western Asia.

Miss Joan B. Procter, F.Z.S.

On the Variation of the Scapula in the Batrachian Groups *Aglossa* and *Arcifera*.

E. G. Boulenger, F.Z.S.

Experiments on Colour-changes of the Spotted Salamander (*Salamandra maculosa*), conducted in the Society's Gardens.

J. Stephenson, D.Sc., F.Z.S.

Morphology, Classification, and Zoogeography of Indian Oligochæta.—I. The Affinities and Systematic Position of the Genus *Eudichogaster* Mchlsn., and some related Questions. II. On Polyphyly in the Oligochæta. III. Some general Considerations on the Geographical Distribution of Indian Oligochæta.

R. Broom, D.Sc., F.R.S., C.M.Z.S.

On the Structure of the Reptilian Tarsus.

Chas. F. Sonntag, M.D., Ch.B., F.Z.S.

A Contribution to the Anatomy of the Three-toed Sloth (*Bradypus tridactylus*).

W. T. Calman, D.Sc., F.Z.S.

Notes on Marine Wood-boring Animals.—II. Crustacea.

The Publication Committee desire to call the attention of those who propose to offer Papers to the Society, to the great increase in the cost of paper and printing. This will render it necessary for the present that papers should be condensed and be limited so far as possible to the description of new results.

Communications intended for the Scientific Meetings should be addressed to

P. CHALMERS MITCHELL,
Secretary.

Zoological Society of London,
Regent's Park, London, N.W. 8.
November 23rd, 1920.

Indian Agricultural Research Institute (Pusa)
LIBRARY, NEW DELHI-110012

his book can be issued on or before ....

Return Date	Return Date